STUDIES OF INHERITANCE IN PISUM.

II. THE PRESENT STATE OF KNOWLEDGE OF HEREDITY AND VARIATION IN PEAS.[1]

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PART I.

INTRODUCTION.[2]

Since the publication of Lock's summary of the genetic work on *Pisum* in 1908, numerous new studies by Tschermak, Hoshino, Pellew and others have very much increased our knowledge of heredity and variation in this genus.

The object of the present review is to summarize this new knowledge and correlate it so far as is practicable with the older knowledge, so that those who are interested may know just how much progress has been made and on what basis of fact the Mendelian analysis of *Pisum* rests.

THE MATERIALS.

The genus *Pisum,* according to the *Index Kewensis,* consists of seven species, possibly only five of which are markedly distinct. The species with their geographical ranges are:

P. arvense Linn., Sp. Pl., 727.—Europe, Asia.

P. elatius Bieb., Fl. Taur. Cauc., II., 151.—Reg. Mediterr.; Oriens.

P. formosum Alef., in Bonplandia, IX. (1861), 237.—Reg. Caucasus, Persia, Asia Minor, Syria.

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These studies on peas are being carried on in collaboration with the Office of Forage Crop Investigations and the Office of Horticultural and Pomological Investigations, U. S. Department of Agriculture.

[2] The writer will welcome corrections and especially desires to have his attention called to any genetic work on peas that has been overlooked.

P. fulvum Sibth.—Asia Minor, Syria.

P. humile Boiss.—Syria, Palestine.

P. Jomardi Schrank.—Egypt.

P. sativum Linn.—Europe, Asia.

P. arvense, P. elatius, and *P. Jomardi,* as grown from seed obtained through the Foreign Seed and Plant Introduction division of the U. S. Department of Agriculture, from various botanic gardens, seedsmen and other sources, are very similar, all having colored flowers, colored seed coats and a similar habit of growth. All three species when crossed produce fertile hybrids. Many students consider the differences between *P. sativum* and *P. arvense* not marked enough to warrant calling them by distinct specific names. Such students regard *P. arvense* as a sub-species of *P. sativum.* The purple-seeded Abyssinian pea is a very distinct form of *P. sativum* or *P. sat. arvense,* differing strikingly in seed and leaf characters from all other forms of this species. *P. formosum* is a perennial alpine form, lacking tendrils and very distinct as regards general habit and seed characters. *P. fulvum* has rusty cream-colored flowers and seeds with black seed coats. *P. humile,* though resembling small-leaved forms of *P. arvense,* gives partly sterile hybrids in crosses with the latter. Experimental work embraced by this review deals largely with forms of *P. arvense, P. sativum* and *P. elatius,* of which there are at least some five hundred varieties known.

About 250 of these varieties have been grown for three years in the experimental breeding plots of the Brooklyn Botanic Garden, where many of the experiments described in succeeding pages have been repeated and confirmed. Most of the descriptions of *Pisum* characters in the following pages are based on notes on these varieties. For help in bringing together this collection, which includes forms from all over the world, I am indebted especially to the Offices of Foreign Seed and Plant Introduction and Forage Crop Investigations of the U. S. Department of Agriculture, Arthur Sutton of Sutton & Sons, P. de Vilmorin, Haage & Schmidt, W. Bateson, C. Pellew, A. D. Darbishire and various botanic gardens of Europe and Asia.

As a whole, the differential characters of these species are sur-

prisingly large in number, though each variety by itself differs from all other varieties, as a rule, in comparatively few of them. In describing these characters and the experiments in connection with them in Part II., they have been arranged in four groups—seed, plant, floral and pod characters. In each of these groups, striking hereditary differences are common.

Thus, the *seeds* vary from 2 mm. to 1 cm. in diameter, with a seed-coat color range from colorless through various shades of green, reddish orange, brown, gray to deep purple. These colors are further varied by color patterns of three types—marbling, striping and stippling. In *plant characters,* still more striking variations are apparent, such as differences in disease-resistance, in height (38–300 cm.), in productiveness (3–4 small pods to varieties with 50–150 pods), in stem color and shape, in leaf shape and color, in number of pinnæ per leaf, in the presence and absence of tendrils, in internode length and number and in time of flowering. The *flowers* differ in size, color, shape, number per peduncle, in position on the flowering axis and in time of pollen maturity. Three colors of *pods* are known. Differences in pod length and breadth range from about 10 by 1.7 cm. to 3 by 0.8 cm. (dry pods) with all degrees of intermediates between. Differences in shape, texture, thickness, toughness, time of maturity for market (45 to 125 days from time of planting) and in number of ovules per pod are striking.

A large number of these variations, as the data presented under Part II. disclose, yet remain to be experimentally studied.

THE RELATION OF ENVIRONMENT TO THE MATERIAL.

It is axiomatic that all organisms live in an environment of some sort. Since the general acceptance of the Mendelian and genotype conceptions of heredity, what part of the organism's characteristics are due to environment and what part are due to heredity have become very important questions for study and experimentation. The Mendelian and genotypical conception that organisms are the expression of fixed and immutable factors or genes, which always (barring mutations) give rise to the same character, provided the environmental conditions remain constant, has led to a new conception of what constitutes a character. A character from this new

view point is a joint expression of factors or of a group of factors and a particular environment. Characters are not inherited, since they cease to exist when unexpressed. Latency, semi-latency, and patency of characters are terms that should be scrupulously avoided in the interests of clear thinking. The older school of biologists and systematists in particular have always regarded all character expressions of a particular kind, such as the white color of flowers in different plant species, the character of stems—whether fasciated or round, the number of floral parts, etc., wherever found, as identical. For example, fasciation, according to de Vries, is a very ancient character, which has been transmitted to many of the higher forms of plant life in a latent condition. In a publication now in press in Germany (98.5) the writer believes he has set forth sufficient evidence to show that fasciations in plants from a genetic standpoint are of many kinds, some of which are hereditary under almost any normal plant environment, while other types only appear as a response to special environments, such as very rich soil, over-watering, or the stimuli derived from insect depredations. Further, these two or more kinds of genetically distinct fasciations, though morphologically indistinguishable, may be present at the same time in a group of plants such as peas. Further discussion of this case will be given in the part devoted to the genetics of *Pisum* stem characters. Morgan and his students (61) evidently look upon a character in this same fashion. They regard the recessive and dominant white color characters of certain breeds of silkworms and poultry as two different kinds of white due to two different genetic factors. White in both races is indistinguishable except in breeding tests. They cite numerous other cases among which is one from Baur illustrating the part environment instead of hybridization may play in showing up this difference. The red primrose (*Primula sinensis rubra*) reared in shade and moisture at a temperature of 30°–35° C. has pure white flowers, while the same plants grown at 15°–20° C. have red flowers. White and red flowers will occur on the same plant if the plants are first allowed to bloom in the cooler temperature and later to continue their blooming under the higher temperature. Another race of primrose (*Primula sinensis alba*) always has white flowers, even at 20° C. The white flower color character of

both races, our systematists and comparative morphologists would say, was the same character (in the absence of the experiments cited above), but many geneticists would look upon them as two genetically distinct characters, one of which is altered by a change in environment. Acceptance of the conception of a character as advanced above may mean a very radical change in the weight which has been placed in the past on comparative morphology and taxonomy as methods for studying the evolutionary history of plants and animals.

THE CATEGORIES OF VARIATION.

Adopting the conception of a character as given above and assuming that plants and animals are made up of hereditary units or factors, variations or character changes in organisms may occur in three ways:

1. Variations due to changes of environment.
2. Variations due to "gain" or "loss" of factors or character determiners through crossing.
3. Variations due to mutation.

1. Variations due to changes in environment are perhaps most clearly illustrated by the change from white flowers to red flowers in *Primula sinensis rubra* following the change in temperature. So far as experimental work goes, change of the same material from one environment to another may take place repeatedly and each time the materials react to the new condition in the same way. Pink-flowered hydrangeas have blue flowers when placed in a soil containing sufficient alum salts. The unbranched varieties of peas are said to branch profusely under the climatic conditions of the Pacific coast region of the United States. Cabbage refuses to head in the tropics. Lock (54) found that seeds of certain pea varieties sown in Ceylon in January and constantly watered produced remarkably stunted plants, which flowered at half the usual height (of seeds sown in November in Ceylon) and bore almost no seed. Examples showing the direct influence of a changed environment could be given by the hundred, did space permit.

2. Changes due to crossing will be illustrated at length in the part devoted to the genetics of *Pisum*.

3. Changes in pea varieties due to mutation will also be discussed under the heading of mutation. Mutations, in the sense used in this paper, are relatively sudden, abrupt variations in a strain of plants which has bred true for more than two generations in the same environment. These variations remain comparatively constant in succeeding generations and form the basis of a new strain or variety. Such characters in peas as white flower color, lack of parchment in the pod, yellow foliage, and absence of tendrils have, so far as we now know, resulted from mutation. Mutations are comparatively common in some organisms and rare in others. Morgan and his students (61) have records of over 200 character changes in the fly, *Drosophila,* resulting from mutation. In peas, this phenomenon, judging by the records, is comparatively rare. Any type of character may be altered or replaced by mutation, the change occurring either as a small or as a large variation.

THE MATERIAL AND THE TECHNIQUE.

" The value and utility of any experiment," says Mendel, " are determined by the fitness of the material to the purpose for which it is used." Mendel (60), Correns (15), and Lock (53) have each expressed themselves strongly regarding the exceptional value of peas as material for the experimental study of heredity. The fact that they possess easily recognized constant differentiating characters, flowers which ordinarily are self-fertilized, and are capable of giving perfectly fertile F_1 hybrids was the chief reason that Mendel chose them. Mendel's reasons coupled with certain other facts, such as the direct economic value of the results, and the quick maturity of the plants, have led to their choice for the present series of studies.

Planting.—Peas are easily grown, and mature as many as three generations a year if both greenhouse and field plots are used. They are sown the 1st of April in this latitude, or earlier if practicable because the late varieties mature poorly under our summer conditions. Wrinkled seeded varieties rot before germination more easily than round seeded varieties. The peas are sown in rows, from 10 to 15 cm. apart in the row, the rows being 1.2 meters or more apart. Only undiseased plump seed are planted, unless there

are special reasons for planting all the seed. The seed are all counted, so that any distortion of ratios from this source can be checked up. Wire netting may be used to keep the tall varieties off the ground. Peas should not be planted on the same ground two successive years, mainly on account of increased liability to pea diseases the second year. Darbishire (21) planted his pea plots to vetch for two years before using them again. Peas may be grown successfully in four-inch (10 cm.) pots or in benches in the greenhouse during the winter months. A bamboo stick or string should be provided for each greenhouse-grown plant. The greenhouse temperature should not be higher than 45°–55° F. Higher temperatures promote trouble with red spider and with various pea diseases.

Crossing.—Crossing in peas is easily accomplished by the removal of the stamens from a half-grown bud and the immediate application of the foreign pollen to the stigma. Pollen may retain its viability in a dry Petri dish for a week or more. Tschermak (81) made successful crosses with 14–21 days' old pollen of Allerfrüheste Mai. Varieties such as Dwarf Gray Sugar and other early-blooming sorts discharge their pollen while the bud is still greenish, while in many of the late-flowering sorts, the flowers are nearly mature before self-pollination takes place (78). Mutilation of the flower rarely causes the flower to fall, and if the crossing is done during sunny weather, most of the crosses will be successful. Under greenhouse conditions, peas have scattering flowers even after the first crop of pods are ripe. These scattering flowers may be utilized to furnish pollen for crosses with late-flowering forms. In field plots, crossed flowers should be protected by square-bottom paper bags. In greenhouse cultures, this precaution is generally unnecessary, especially in winter. Diluted grain alcohol is used to kill stray pollen on hands and the instruments after each cross. Usually the pollen to be applied is carried on the stigma and this foreign stigma brushed across that of the flower to be crossed. In labeling the cross, each plant of a variety is given an individual number, and care is taken so that each plant used in crossing also bears several uncrossed pods. The maternal parent is designated first.

Self-fertilization.—Because peas are naturally self-fertilizing, protection of the flowers of both pure strains and hybrid generations

is ordinarily unnecessary. The few recorded changes of chance crossing are probably due to the pea weevil (*Bruchus pisi*) (60, 78) or to thrips (3, 78). In case the pollen of a flower is ineffective, the stigma may extend itself beyond the keel and chance crossing come about in this way. No cases of the latter type are recorded and the possibility of error from this source is rare (60).

The source of error from chance crossing in a locality may be tested out by growing several hundred plants of a variety with green cotyledons side by side with a row of a pure yellow cotyledon strain. When the seed of the green cotyledon strain are mature, the per cent. of crossing can be calculated from the number of yellow seeds found on the green-seeded plants. In an examination of over 10,000 seeds of several green-seeded varieties at the Brooklyn Botanic Garden, not a single case of cross fertilization came to light. Bateson and his students (5), Messrs. Sutton (5), Tschermak (81) and Mendel (60) each record a few cases, the per cent. in each case being much less than ½ per cent. The few non-conformables in Lock's experiments (54) on cotyledon color are attributed by him to errors in labeling, planting and to improper maturing.

Because peas are naturally self-fertilizing, pure lines may be selected from almost any of the commercial varieties with the assurance that they will be constant as regards visible characteristics and relatively free from heterozygosis almost at once. Most of the varieties at the Brooklyn Botanic Garden have given constant strains after at most two years of selection, while the great majority were constant from the start. In judging constancy, only characters such as flower color, seed shape and color, foliage color and shape of pod, which are but slightly influenced by small environmental changes, were used. Tschermak (78), Macoun (57.5), Hurst (42), Sherwood (72), Knight (50), Darwin (22) and many other experimenters have often remarked upon the exceptional constancy of pea varieties. It should be noted that pea varieties commonly grown for forage purposes have generally become very much mixed mechanically with each other as well as with various vetches through carelessness in handling and harvesting. Often it is possible to select ten or more constant varieties from a handful of such seed.

Labeling and Recording.—The system of labeling used in the

work carried on at the Brooklyn Botanic Garden consists in giving the commercial stock of a variety as received a number such as Pisum 12; the plants grown from seed of P12 are numbered P12–1, P12–2, P12–3, etc. The next generation of P12–1 being recorded as P12–1–1, etc. Crosses are designated thus: P12–1 × P14–1, the F_1 progeny as (P12–1 × P14–1)–1, –2, –3, etc. In F_2 and subsequent generations all seeds planted are counted, and plot sketches kept of the arrangement of the plantings. A printed description blank covering all the common characters of peas is used for records of individual plants, and less detailed blanks for cultures studied for special characters.

Harvesting.—In studying seed characters extreme care should be taken to allow proper conditions for maturity. Harvesting immature peas may lead to considerable errors in studies on cotyledon and seed-coat color. Pea vines may be allowed to mature until no green remains and they are dry and brittle. This insures maturity. In order to avoid breaking such brittle material, the vines should be thoroughly wetted with a hose before handling. Each plant should be labeled with a tag label as gathered. Green cotyledon varieties tend to fade to yellow if left exposed to light for a considerable time (54) and damp wet weather at harvest time may bring about the same result much sooner (1, 60, 21).

Environment.—No factor is of more importance in a detailed genetic study of the characters of a group of plants such as *Pisum,* than environment. Environment, being the co-partner of heredity in the make-up of a character, should have just as precise a description as the characters themselves, or else be eliminated altogether by growing the material under as near as possible the same conditions. If environment were as easy a proposition to handle as in the case of chemical experiments, one could define it in the case of each experiment with such exactness that it could be easily reproduced. Unfortunately this is not practicable, because of the many factors which compose it. Under greenhouse conditions, it is more practicable than in field cultures. However, even here, aside from the temperature, watering, etc., factors such as soil and light vary so over an area when large cultures are grown, that it is largely a figure of speech to speak of absolute uniform environment for the whole area.

In order to secure the greatest uniformity practicable in environmental conditions, all cultures which are studied from a comparative standpoint are planted in the same batch of soil, at the same time, and given the same cultural care. A few characters of *Pisum* such as flower color, presence of parchment and presence of tendrils are very little affected by environmental fluctuations. The majority of *Pisum* characters, however, react to environmental fluctuations so as to give rise to error in any intense study, unless the fluctuations are known well enough to be taken into account. By growing a large series of cultures, both hybrid and pure line, under approximately the same set of conditions by the method mentioned above, and securing as near as practicable the same conditions for several years, one may become so familiar with the factors composing such an environment and the reactions of the plants to such an external set of conditions, that the environment itself may be used as a standard by which the modifications of the same plants grown under other environments may be described. Such an environment may be called a *standard environment*, as it is the criterion by which the effect of all other conditions on characters is decided. Whether such a standard can be made precise enough to be of much value in genetic work remains to be seen. If one describes character changes by revolving round a circle, one gets nowhere, and without a standard starting place, one simply revolves. The older biologists used the term normal to designate in a vague way what I mean by standard. Normal environment, however, may mean almost any common environment in experimental work. Thus there is no gain in preciseness through its use.

PART II.

THE GENETICS OF *Pisum*.

Genetic studies on the genus *Pisum* may be divided into two groups—those made before and those made since the rediscovery of Mendel's law in 1900. The pre-Mendelian studies resulted in a great deal of practical good, but were of slight scientific value, since no laws of heredity were discovered. The post-Mendelian work is as yet too young to have given great practical results. Laws

have been discovered however, which ultimately may lead to un-dreamed practical possibilities.

HEREDITY STUDIES ON *Pisum* PRIOR TO 1900.

According to Darwin (22), as early as 1729, white- (yellow cotyledons) and blue- (green cotyledons) seeded varieties of peas had been observed (probably through insect crossing) to give rise to pods containing both blue (green) and white (yellow) peas. In 1787 Andrew Knight (50) had crossed various races of peas and originated many new varieties, some of which, *e. g.*, Knight's Tall Wrinkled Marrow, are said (42, 72) to have persisted in a prac-tically unmodified form, but under different names (British Queen), down to the present day, representing, if true, a striking illustration of the constancy of an old variety, through a hundred years or more of inbreeding. Knight, in many ways, was a forerunner of Mendel, as he had observed the dominance of tallness in peas over dwarfness, purple flower color over white flower color, gray brown seed coats over uncolored seed coats and the breeding true of re-cessives and part of the dominants. But he was unaware of the significance of these facts and of the importance of determining the ratios of the various kinds in the second and third hybrid genera-tions. He is credited, however, by Sherwood (72) with having given us the start in wrinkled seeded varieties of peas, as before his time wrinkled peas appear to have been unknown.

Goss in 1822 (36, 21) also anticipated Mendel by his observa-tions on the cotyledon colors of peas, *i. e.*, the dominance of yellow over green cotyledons in the first hybrid generation and the occur-rence of green and yellow peas in the same pods in the second hybrid generation, as well as the subsequent breeding true of part of the yellow seeds and all of the green seeds in later generations. Appended to Goss's description of his results is an editorial com-ment giving the results of crossing green and white (yellow) peas by one, Mr. Seton. Seton used the green-seeded Dwarf Imperial as the maternal parent in a cross with a (white) yellow-seeded va-riety. Four peas were obtained, which, though subsequently proven to be true hybrids, did not differ in appearance from the uncrossed seeds borne by the Dwarf Imperial plant. Thus even at that early

stage in the history of genetics, complication and confusion appeared on the scene. Bateson (21, p. 198) has since shown such varieties as the Imperials to have opaque green seed coats and yellow cotyledons. Seton's observations were on seed coat color, while Goss dealt with cotyledon color. Like Knight, however, Goss did not see the significance of his results nor did he determine the numerical proportions of the two colors of seed in the F_2 generation.

Gaertner (35) also made pea crosses, as well as crosses of many other plants. He interpreted the dominance of yellow cotyledon color over green as due to xenia (the direct and immediate effect of the male parent on the maternal tissues), not apparently aware that the characters yellow and green seed color were those of the embryo of a new generation.

Darwin (22) grew and crossed peas and noted the extreme vigor of F_1 hybrids as compared to the parent forms growing beside them, and studied variation and inheritance in several characters of peas. He had, however, never heard of Mendel's work.

Laxton (22) and others had noticed the rather remarkable constancy of pea varieties, a number of which were known to be twenty or more years old. Laxton (the ancestor of the present well-known family of pea and fruit breeders) also furnished Darwin with data on the relation of environment to the production of double flowers in peas, as well as data on the inheritance of such characters as purple pod and seed color.

Masters (59) wrote letters to the *Gardner's Chronicle* against the practice (unfortunately still quite common) of changing the names of old varieties, so as to increase their sales. Judging by the printed replies, his accusations were very much resented by the seedsmen. Masters introduces one of his communications by this quaint reference to his own qualifications as a pea specialist, "And first let me give you my pretensions to pass an opinion upon the matter, that, with your readers (to whom I am unknown), I may stand in a fair position. Be it known, then, that forty years ago, my father, of good memory, employed my then young eyes to detect the differences of the peas he intended for seed, and many a patient hour was devoted to this most necessary of operations under his guidance" (1850). Masters also claims (22) to have raised four distinct sub-varieties from one plant—

> Plants bearing blue and round seeds,
> Plants bearing blue and wrinkled seeds,
> Plants bearing white and wrinkled seeds,
> Plants bearing white and round seeds.

The remarkable part of Master's claim, however, is that though he grew the four varieties separately for several successive years, each kind always produced all four kinds mixed together. In other words, not one of these varieties bred true as regards the four characters mentioned, while according to most of the recent studies, wrinkledness and green cotyledon color (blue) should be constant. White (98) has recently secured results which possibly may throw some light upon Masters's claim as far as the inheritance of cotyledon color is concerned.

Though facts were apparently plentiful (such as they were), regarding the effects of environment and the heredity of characters in peas and other plants, efforts to formulate them into a *law of heredity* that would stand the test of experimental inquiry were, prior to the studies of Mendel, apparently futile. Heredity, says an old writer, is a collection of facts without laws, while Balzac wrote " heredity is a maze in which science loses itself."

Mendel's own results on the inheritnace of characters in peas were published in an obscure Austrian natural history society's proceedings, and except for a few lines in Focke's book (28) on hybrids, and a bibliographical reference in Bailey's " Plant Breeding," they remained lost until 1900, when the three botanists—Correns (14), Tschermak (78), and de Vries (23.5)—rediscovered the law and resurrected Mendel's paper from oblivion. The subsequent impetus this rediscovery and resurrection gave to the scientific study of plant breeding is abundantly exemplified by the thousands of papers and books published since 1900 containing results of experiments on hundreds of varieties of plants and breeds of animals. In corn alone, the inheritance of over thirty characters has been studied and found to be consistent with Mendelian principles. In tobacco, cotton, sweet peas, corn, wheat, oats, and poultry results of considerable practical value have been obtained by the use of Mendelian methods.

MENDEL'S LAW.

The fundamental principle of Mendelism is very simple and rests upon the assumption that animals and plants are made up of units (called factors, genes, determiners, etc.), and that these units may separate in the formation of the " germ-cells " (pollen and eggs) of the hybrid offspring without having had any permanent influence upon each other. The assumption that such units or factors exist is based upon experimental data derived from crossing two plants or animals from true breeding strains differing in two or more characters and the growing of at least three subsequent hybrid generations under approximately the same environment as the original two ancestors of the cross. For example, when two strains of peas, one constant for purple flowers and green cotyledons and one constant for white flowers and yellow cotyledons, are crossed, the first or F_1 generation is uniformly all purple-flowered with yellow cotyledons. Self-fertilized seed from any of these F_1 plants, if sown in sufficient numbers, will produce approximately 9Pfl.YC: 3Pfl.GC: 3Wfl.YC: 1Wfl.GC plants, showing that the determiner for green cotyledons in addition to separating from its F_1 associate—the determiner for yellow cotyledons—also is inherited independently of its ancestral associate—purple flower color. Mendel himself regarded purple and white flowers in peas as a pair of characters, one of which completely dominated the other. Geneticists now largely hold to the presence and absence hypothesis, by which the purple is regarded as due to the presence of a factor or determiner for purple in the one strain and the white-flower character as due to the absence of this determiner or factor for purple color. Data from genetic experiments, most geneticists believe, are more simply expressed by the presence and absence concept.

Since the promulgation of Johannsen's genotype hypothesis, many geneticists believe these Mendelian factors to be unmodifiable by selection and selection itself to be but a process of sorting out or freeing hybrid or mixed populations from heterozygosis.

MENDELIAN STUDIES OF PEAS.

Sixteen years have elapsed since the study of heredity assumed the dignity of a separate science under the name of *genetics*. Dur-

ing these sixteen years much has been accomplished through experimental studies on peas and other organisms. Many complications in the application of Mendel's law to data from these studies have arisen, most of which have served to place the Mendelian conception of heredity on a still firmer foundation [see (61)].

Among peas, over thirty-two different types of characters have been experimentally studied, amounting in all to over 75 single characteristics of *Pisum*. In about half the cases, the knowledge gained is somewhat fragmentary. In the other half, owing to the painstaking work of Mendel, Bateson, Vilmorin, Darbishire, Lock, Correns, Gregory, von Tschermak and others, the characters have been put upon a factorial basis. In the list of characters studied which follows, the factors are designated according to the presence and absence conception, small letters standing for absences. Where the use of the letters for the factors given by the investigator of the character concerned, is practicable, they have been retained. In cases where this is inconsistent with the scheme of a complete analysis of the genus *Pisum* upon a factorial basis, new letters have been substituted. In many cases these refer to adjectives descriptive of the part they play in the formation of the character.

In the case of some of the factors given in Tables I. and II., the data hardly justify their consideration. However, since the data upon which each factor determination is based are to be given in the following pages, the writer justifies putting them in the tables in the belief that further research concerning them will be more quickly inspired.

For the cause which this paper represents, it probably would be better if all the crosses thus far made were given under each character description. Space at present, however, forbids this. So that in the following pages, under the character description, will be given the varieties studied, the results of the crosses in terms of dominance and ratios, the factorial interpretation, the effect of the environment, if any, on the factorial expressions, and any remarks or adverse criticisms.

Reciprocal crosses in plants give the same results in all but a few cases, and these few cases in *Pisum* are described. Otherwise the reciprocal of a cross, although often made, is not specifically consid-

TABLE I.

CHARACTERS IN *Pisum* UPON WHICH EXPERIMENTAL STUDIES HAVE BEEN EXTENDED ENOUGH (IN MOST CASES) TO FORM THE BASIS FOR GENETIC FACTOR REPRESENTATION.

No.	Type of Character.	Characters and their Corresponding Factors.	Reference to Bibliography.
	Seed characters		
1.	Seed coat color...	Gcjh (brown to yellowish green, gray), gcJ (colorless), U (purple), light orange brown (GcjH), dark brown (GcJ)	(1, 2, 3, 14, 21, 33, 43, 50, 54, 55, 60, 78, 79, 81, 83, 86, 90)
2.	Seed coat color pattern		
	Purple spots.....	EF (purple spots), Ef, eF, ef (no purple spots)	(1, 2, 3, 14, 21, 34, 43, 51, 54, 55, 60, 79, 81, 83, 86, 89)
	Violet eye.......	N (violet eye), n (absence)	(86)
	Black eye	Pl (black eye), pl (absence)	(14, 56, 57.5, 90)
	Mapling.........	M (mapling), m (absence)	(1, 3, 21, 43, 54, 55, 60, 86)
3.	Seed coat surface	L₁L₂ (indent), L₁l₂, l₁L₂ (smooth)	(3, 37, 43, 54, 55, 81, 83, 86)
4.	Seed shape	R (round), r (angular, wrinkled) (smooth)	(1, 2, 3, 14, 19, 21, 23, 33, 37, 42, 43, 48, 54, 56, 59, 64, 72, 79, 80, 81, 83)
5.	Seed size........	Not sufficiently studied	(1, 57.5, 86, 89, 90, 96)
6.	Cotyledon color..	YGI, Ygi (yellow), YGI (green)	(1, 2, 3, 7, 14, 21, 22, 33, 35, 36, 38, 42, 43, 52, 53, 54, 56, 59, 60, 78, 80, 81, 83, 90, 96, 98)
7.	Cotyledon starch	R (simple oval), r (compound, round)	(Same as No. 4)
8.	Starch modifier...	Very slightly studied	(48)
9.	Starch water content	R (low), r (high)	(3, 19, 21, 23, 39, 48)
10.	Cotyledon starch content	R (high), r (low) (high sugar content)	(Same as Nos. 4 and 9)
11.	Wet, cold weather germinating ability	R (excellent), r (low)	(Various seedsmen)
	Plant characters		
12.	Height..........	TLe (tall), tle (dwarf), tLe, Tle, (half dwarf or talls?)	(1, 2, 3, 7, 21, 22, 33, 43, 49, 50, 52, 54, 56, 60, 79, 80, 81, 83, 85, 90)
13.	Leaf axil color....	CD (colored axil), cd, Cd (no axil color)	(3, 16, 43, 54, 55, 56, 60, 74, 81, 86)
14.	Stem...........	Fa (non-fasciated), fa (fasciated)	(1, 3, 8.5, 21, 25, 56, 60, 74)
15.	Inflorescence.....	Fa (axillary), fa (umbellate)	(1, 3, 8.5, 21, 25, 56, 60, 74)
16.	Stem thickness...	T (robust), t (slender)	(49, 54)
17.	Internode length.	Le (long), le (short)	(1, 49, 54, 78)
18.	Time of flowering	Very complicated, not sufficiently studied	(3, 9, 39, 40.5, 43, 49, 54, 60, 66, 81, 83, 84, 85)

TABLE I.—*Continued.*

No.	Type of Character.	Characters and their Corresponding Factors	Reference to Bibliography.
	Plant characters		
19.	Flowers per single peduncle	Fn (one flower or 1–2 flowers), fn (two–three flowers per peduncle)	(90)
20.	Leaf terminals...	Tl (tendrils), tl (no tendrils, Acacia)	(64, 88, 89, 90)
21.	Leaf size........	Not sufficiently studied	(48, 54)
22.	Foliage and stem color	O (green), o (yellow)	(3, 21, 43, 60)
23.	Bloom	BlW (glaucous), blw, Blw, blW (glabrous)	(86, 90, 92)
24.	Productivity.....	Very complex, not sufficiently studied	(39, 44, 54, 66, 68–70, 76–77, 93, 94–95)
	Flower character		
25.	Flower color.....	AB (purple), Ab (rose or pink), aB, ab (white)	(1, 2, 3, 16, 21, 33, 40.5, 43, 53–56, 60, 78, 81, 82, 83, 84, 85, 86, 90)
	Pod characters		
26.	Color	P₁P₂ (purple), Gp (green), gp, P₁p₂, p₁P₂ (yellow)	(3, 14, 21, 22, 34, 43, 56, 60, 83, 86, 90)
27.	Apices	Bt (blunt), bt (acute)	(1, 3, 5, 42, 54, 56, 80, 81)
28.	Shape..........	PV (round, smooth, inflated), pv, Pv, pV (constricted)	(1, 2, 3, 21, 22, 43, 54, 56, 60, 80, 81, 86, 90, 99)
29.	"Chenille"......	S (free), s (chenille)	(92)
30.	Pod texture......	PV (parchment), pv, Pv, pV (non-parchmented)	(Same as No. 28)
31.	Edible	PV (non-edible), Pv, pv, pV (edible)	(Same as No. 28)
32.	Curved or straight	Not sufficiently studied	(5)
33.	Broad or narrow .	" " "	(43, 54, 56, 80, 81, 90)
34.	Ripening........	" " "	(43, 77)

ered. Where the expressions constant or breeding true are used in regard to inheritance of characters, mutation phenomena are always excepted.

TABLE II.

LIST OF *Pisum* FACTORS, ALPHABETICALLY ARRANGED, AND THEIR CORRESPONDING CHARACTER EXPRESSIONS.

Factor.   Expression.

1. A   Salmon pink or rose flower color. With CD gives reddish leaf axils.

2. B   Purpling factor + A gives purple flowers. With CD + A gives purplish leaf axils.

3. Bl   Glaucous foliage, stems and pods (with W).

4. Bt   Pods with blunt apex.

5. C (A)   With D gives leaf axil color.
6. D   With C gives leaf axil color.
7. E (A)   With F gives purple dotting on seed coats.
8. Ef   Modifies the expression of Lf toward earlier flower-
             ing.
9. F   With E gives purple dotting on seed coats.
10. Fa   Axillary flowers, round stems.
11. Fn   One-two flowers per peduncle.
12. Gc (A)   Yellowish green to grayish brown seedcoat color
             (weak chromogen factor), brown hilum.
13. G   Green cotyledon pigment.
14. Gp   Green pod color.
15. H   Brightener or inhibitor of expression of Gc.
16. I   Factor which causes green cotyledon color to fade.
17. J   With Gc gives dark brown seed coat color.
18. K(?)   Partial inhibitor for R (starch).
19. L_1 (A)   With L_2 gives indent peas.
20. L_2 With L_1 (A) gives indent or dimpled peas.
21. Le   Long internodes; with T gives tall plants.
22. Lf   Primarily responsible for late flowering.
23. M   Brown or maple mottling on seed coat; or "ghost
             mottling" in absence of A.
24. N   Violet eye on seeds.
25. O   Green foliage, stems, and pods.
26. P   Inflated, parchmented, non-edible pods with V.
27. P_1 With P_2 gives purple pods.
28. P_2 With P_1 gives purple pods.
29. Pl   Black eyed peas.
30. R   Round, smooth seeds with simple, oval starch grains,
             low water content.
31. S   Pods with seeds separated or free.
32. T   Tall, robust plants; large number of internodes (over
             20).
33. Tl   Leaves with tendrils.
34. U   Dark self-colored purple seed coat.
35. V   With P, parchmented, smooth pods.
36. W   With Bl gives glaucous foliage, pods, etc.

Factors A, C, E, Gc and L₁, so far as our present knowledge is concerned, appear *absolutely* coupled and it is much simpler to regard them all as one factor (*i. e.,* A) with many separate expressions.

1. SEED COAT COLORS.

The seed coat characters include the various testa colors and patterns. Testa color and pattern are so closely associated that they are described together. Unlike similar patterns in seeds of other plants, such as beans, the colors do not appear to be independent of the pattern, except possibly in the case of the eye or hilum pattern color. One never finds purple marbling or maple-brown stippling among the seed coat colors of *Pisum.* The stipple pattern is always purple and the marbling pattern is always brown. The seedcoat colors of the varieties of peas thus far genetically studied are five in number—colorless to greenish white, deep to pale green, dull green or gray to brick red or grayish brown, dark brown, orange brown and violet or dark purple.

Colorless seed coats are always associated with white flowers, uncolored leaf axils. When such seed coats are separated from the rest of the seed, they are somewhat transparent with traces of yellow and green present. This is the common seed coat color of white-flowered varieties.

Green seed coats genetically are at least of two different kinds, one common to white-flowered varieties, such as the Imperials (21), Fillbasket and Telephone (1); the other present in a variety with colored flowers and received under the erroneous name of *P. Jomardi.* In the first case, the green testas may bleach on ripening, especially in piebald cotyledon sorts such as Telephone (1). Fillbasket testas (1) rarely bleach. Nothing is known concerning the genetic behavior of the *P. Jomardi ?* type. Telephone green is soluble in alcohol.

Gray seed coat color is always associated with colored flowers. The color varies from dull green through gray to brick red to dull brown, the variation resulting from environment. The redness and brownness are due to exposure to the sun or moisture when ripening (1). In dull years, Bateson says scarcely any turn red. Peas grown in the greenhouse and harvested in winter very rarely,

in my experience, turn brown or red.   The red can be eliminated by
boiling, which will leave the seeds thus treated gray (1).   Gray
chemically (55) is determined by a greenish pigment contained in
all or almost all the seed coat cells.   With but three or four possible
exceptions, all colored flowered varieties have seeds with gray pig-
ment.

Orange brown or light yellow orange seed coat color is charac-
teristic of several varieties of field peas with colored flowers de-
scribed by Tschermak (86) as *P. arvense* nos. VI., IX. and X.   With
age and exposure, they turn browner.

Dark brown seed coat is a dark chocolate brown typical of the
red-flowered Kneifel pea with purple pods experimented with by
Tschermak (86) and Haage and Schmidt's Kapuziner.

Violet or *dark purple* seed coats are of two different kinds, one
apparently what Emerson (27.5) would call a recurring mutation,
which results from an extreme variation of the purple spot pattern
to a self-purple and the subsequent breeding true of them (34).
The other type of purple seed coat is a constant characteristic of sev-
eral varieties of field peas, particularly of No. 24894 (29), the " black
Abyssinian " pea of the U. S. Department of Agriculture.   The
genetics of the first type is taken up under the seed coat color pat-
terns of *Pisum*.   That of the latter type is only mentioned, so far
as I am aware, in Vilmorin's list (90) where it is recorded as a
dominant to various other seed coat colors.

The seed coat patterns of *Pisum* are three in number—a purple
stippling or dotting, a brown marbling, and an eye pattern.

Purple dotting or *stippling* is only found in association with races
with colored flowers and gray seed coats, although many colored-
flowered varieties do not have seeds with purple dots.   The dots
themselves often transgress the limits of dots, resulting in splotches
and, in extreme cases, wholly self-colored peas (1, 22, 34, 81,
86).   In the seeds with gray seed coats which have turned red or
brownish, the purple dots are often obliterated (1).   The purple
color according to Lock (55, 56) is a cell-sap pigment, confined
to certain large cells of the sub-epidermal layer.   This fact accounts
for its diffusion into blotches and traces and its complete oblitera-
tion when the seeds are left exposed to damp, sunshiny weather

conditions.   Fruwirth (34), however, describes this pattern in the Blauhülsige variety as due to brownish, weak violet pigment granules in the palisade cells.   Lock says this pigment is easily soluble in boiling water.

Brown marbling or the *maple* pattern, as the English call it, is associated only with colored flowers as far as the color is concerned. Lock, however (54, 55), finds the pattern itself ("ghost mapling") without coloring, may be associated with white-flowered plants.   The brown pigment of the maple pattern is largely confined to the cell walls of the outermost layer of I-shaped testa cells (55).   The pattern color deepens with age and is insoluble in boiling water.

The *"eye" color* pattern is characteristic of both colored and white-flowered pea races.   The color is present as a deep black at the point of attachment, with a dark sooty tint usually present over the seed as a whole.   Some varieties have brown coloring (81) in place of the black while other varieties are without color at this spot. The brown hilum color according to Tschermak is always associated with colored flowers and colored seed coats, so it may be considered as simply another of the numerous expressions of factor A.

Violet eye is due to a violet hilum pigment, characteristic particularly of a race of Victoria peas with which Tschermak experimented.

Brown marbling, purple dotting or stippling and black eye may all be associated in the same pea seed coat.   In fact, a couple of wild species obtained direct from Asia have seeds characterized by all three of these color patterns.

VARIETIES STUDIED.

Varieties with *colorless* or almost colorless seed coats as described under colorless: Grünbleibende Folger, Désirat, Auvergne, Yellow-podded Sugar Pea, Express, Emerald, Victoria, Svalöf Small Green-seeded *Pisum,* Prince of Wales (Tschermak, 81, 86) ; Grün Späte Erfurter Folger (Correns, 14) ; Laxton's Alpha, Veitch's Perfection, Sunrise, British Queen, Victoria Marrow, Trés nain de Bretagne, Earliest Blue, Ceylon Native No. 1, Satisfaction, Ringleader (Lock, 54, 55, 56) ; Serpette, British Queen, Victoria Marrow, Ringleader, Nain de Bretagne (Bateson, *et al.,* 1), White-flowered Mummy (Macoun, 57.5).

Green seed coat varieties: Telegraph, Telephone, Fillbasket (Lock, Bateson and Kilby, 1, 54).

Gray seed coat, violet stippling: Graue Riesen, Svalöf *P. arv.,* IV. (Tschermak, 81, 86); Sutton's French Sugar Pea (Lock, 53); Blauhülsige (Fruwirth, 34).

Gray seed coat, maple marbling: *P. arv.,* IX., *P. arv.,* X. (Tschermak, 81, 86); Irish Mummy (Bateson, 1).

Gray seed coat, violet stippling, maple marbling: Ceylon Native Pea No. 2 (Lock, 54).

Gray green, bright orange tint: Svalöf *P. arv.,* VI., *P. arv.* No. VII., *P. arv.,* IX. ?, *P. arv.,* X. (Tschermak, 81–86); Pahlerbse with purplish pods, Purpurviolettschottigen Kneifelerbse (Correns, 14).

Dark brown seed coat: Red-flowered Kneifelerbse with purple pods—Tschermak, 86.

Brown hilum: P. arv., VI., *P. arv.,* VII., *P. arv.,* VIII., *P. arv.,* X.—Tschermak, 81, 86.

Violet eye: P. arv. No. IX., violet-eye Victoria—Tschermak, 81, 86.

Black eye: In most cases varieties not given. Black-eyed Marrowfat—Macoun, 57.5; Haage & Schmidt's Kapuziner, Bohnenerbse (H. & S.), Lyngby Fall Pea (U. S. Dept. of Agr.), Benton (U. S. Dept.), Prince (S. P. I. 22046, U. S. Dept.)—White (unpublished data).

<div align="center">RESULTS FROM CROSSING.</div>

Colorless × colorless seed coat always gives colorless or transparent seed coats (1).

Colorless × green or white (opaque) gives various results, but never fully opaque seed coats. In some cases the F_1 hybrids are colorless, in others intermediate as regards opaqueness and the presence of pigment.

Opaque × opaque (1) always gives F_1 progeny with opaque seed coats.

Colorless × gray brown seed coat always gave all gray browns in F_1. In the F_2 generation, the following results have been obtained:

Investigator.	Gray Brown.	Colorless.	Total.	Ratio.
Mendel.....................	705	224	929	3.15 : 1
Lock......................	87	24	111	3.62 : 1
Bateson and Lock..........	50	19	69	2.63 : 1
	842	267	1,109	3.15 : 1
Lock F₃..................	231	85	316	2.71 : 1

F_4 generation grown by Lock but actual figures not recorded.

In addition to the figures given above are those from crosses made by Correns, Tschermak and others. These data are omitted here because either the exact figures are not given in the original papers or that these figures are scattered through so many papers and so often repeated as to make their accurate collection impracticable.

In F_3, a certain proportion of the F_2 segregates with colored seed coats breed true, another portion break up, giving again the 3 : 1 ratio, while the F_2 segregates with colorless seed coats breed true.

In certain crosses made by Tschermak (86) between colorless and gray brown (whitish brown) seed coat varieties, F_1 progeny with dark brown seed coats were obtained, which in F_2 gave dark browns, grays and colorless seed coat segregates, approximating the proportion 9 : 3 : 4.

Colorless × gray seed coat with purple dots gives in the next (F_1) generation, all gray purple dotted seed coats. In F_2, the following results have been obtained:

Investigator.	Gray and Purple Dots.	Gray.	White.	Total.	Ratio.
Lock (53, 54)........	68	19	24	111	9 : 5.7
Tschermak (86)	71	46		117	9 : 5.8

F_2 heterozygotes in F_3 gave:

Investigator.	Gray and Purple Dots.	Gray.	White.	Total.	Ratio.
Lock..............	178	53	85	316	9 :6 .9

In F_4, Lock (55) tested out the genetic nature of non-purple dotted colorless seed coat F_3 segregates which had bred true in F_4

by crossing them with various F_4 segregates breeding true to gray seed coat color.

In F_5, from 60 crosses of colorless F_4 × gray F_4,

  9 crosses gave 21 gray purple dotted : 23 gray,

  23 crosses gave only gray purple dotted,

  28 crosses gave only grays without purple dots.

Tschermak (86) has made numerous crosses between pure varieties and extracted F_2, F_3 and F_5 segregates with and without the character purple dotting. In these crosses, *colorless* × gray without purple dotting in some cases gave all purple dot progeny in F_1 (agreeing with the results of Lock's crosses above). In other cases, using different varieties, Tschermak always secured only non-purple-dotted progeny both in F_1 and in F_2, except in certain very exceptional cases. In these exceptional cases purple dotting appeared sporadically on the seed coats of gray segregates which had bred true to a self gray for several generations, while on the other hand there were cases in which purple dotting was expected, but failed to appear when certain crosses were made (86, S. 160). Varieties (86) practically breeding true to the absence of purple dotting also occasionally have a few seeds with purple dots, and these appear on plants the majority of the seed of which is without the purple dots.

Colorless × orange-brown or greenish orange tinted (*e. g.,* P. *arv.* Svalöf No. VI.) gave in F_1, in Tschermak's experiments (86) progeny with dark brown seed coats with purple dots. In F_2, 4 classes appeared—dark brown with purplish reddish dots, dark brown with no dots, whitish brown (gray) with no dots, colorless. The numbers were small, hence the ratios are not of much importance, except in showing that the dark browns were in greater number than the other two classes. The gray segregates were constant and in back-crosses with the colorless seed coat parent gave only dark browns, grays and colorless seed coat segregates, with or without purple dots, as in Lock's crosses of F_4 colorless and F_4 gray seed coat segregates given above. If large enough numbers had been obtained Tschermak (86, S. 161) believes the orange-tinted grandparental type would have appeared again.

Correns (14) crossed a colorless seed coat variety with two

varieties having orange-red seed coats and obtained in F_1 progeny with seed coats varying from almost colorless ? to intense orange-red—the variation in coloring often occurring in the peas of the same pod. All were more or less purple spotted. These gave, in F_2, 3 classes, the two grandparental types and the F_1 type. The statement regarding the presence of purple dotting on these F_2 segregates is rather obscure.

Lock (53, p. 326) does not consider orange-brown testa color as a separate character from gray-colored testa, and Bateson thinks Corren's exceptional results in F_1 of the cross just described may be due to environment. The writer has distinctly orange-red seed coat peas with white flowers in his collection from Chile and he hardly believes that present data justify Lock's contention, because these peas do not mature as gray under the conditions in which ordinary gray seed coat varieties have gray seeds.

Colorless × dark brown seed coat varieties should according to Tschermak's formula for at least one such variety [redfl. Kneifel-erbse, S. 181 (86)] give all dark brown seed coat progeny in F_1 with or without purple dots, depending on the colorless variety used. I have not, however, been able to find the published record of the data upon which this formula is based. True breeding (86) dark brown seed coat segregates crossed with colorless give dark brown in F_1.

Colorless × gray with maple pattern gives in F_1 maple pattern either with or without purple dots. The presence of the purple dots in F_1 of such a cross as this is altogether dependent on the kind of colorless seed coat variety used, as the genetic evidence from Bateson (1), Tschermak (86) and others shows that a gray maple pattern seed coat variety may be crossed with colorless and give maple and purple dots. The same maple variety may again be crossed with a colorless, but this time a different one and give only maple. Bateson (1) found British Queen to be a colorless seed coat variety of the first type and Victoria one of the second type. Tschermak [see Bateson (1)] secured 2 cases where Victoria × unspotted varieties gave purple spots in F_1, while reciprocals of the same cross gave unspotted seed coats. In Tschermak's latest publication (86) on the subject, two varieties of Victoria are recognized,

one of which will give purple dots in F_1 as above and one of which would only give maple as found by Bateson.

Tschermak (86) secured in F_1 from maple $\times$ colorless, brown maple seed coat without purple specks. These F_1's gave in F_2, 52 maples : 17 dark brown selfs : 1 ghost maple : 6 colorless.

In F_3,

F_2 *maples* gave in one case all 4 classes; in another case only 2 classes—maples and colorless.

F_2 *dark browns* gave 6 brown : 1 colorless in one case; in another 7 browns : 1 colorless.

F_2 *ghost* maple gave 9 ghost maple : 3 colorless. Ghost maples are hard to distinguish from whites, so Tschermak believes the F_2 classes above approximate the ratio 9 maple : 3 brown : 3 ghost maple : 1 colorless.

F_2 *ghost maple* segregates $\times$ a pure colorless *P. sativum* race gave in F_1, 4 ghost maples : 2 colorless.

In F_2, one of these ghost maples gave ghost maples which bred true in F_3 and F_4, while another one ("spur" ghost maple) gave 2 like itself and 7 without mapling. One of the colorless F_1 individuals gave 2 ghost maples and 6 colorless. In a similar cross, only spurious ("spur") maples and colorless were obtained in F_1, the "spur" ghost maples giving 2 "spur" maples : 7 colorless in F_2. Tschermak believes these "spur" maples are due to the inactivity of the determiner for mapling. Fruwirth and Tschermak both have observed exceptional cases where mapling has appeared in the descendants of non-mapled peas.

In back-crosses of segregates from mapled ancestors,

Brown $\times$ colorless never gave maple,
Brown $\times$ brown never gave maple.

Certain peculiar ghost maples on plants with rose or pink flowers $\times$ white-flowered ghost maples gave in F_1 and F_2 no maples.

In reciprocal crosses between segregates of *P. arv.* $\times$ *P. sat.* involving the maple pattern, F_3 brown $\times$ ghost maple and reciprocal [Table 22 (86)] gave in F_1, except in one case, always browns, the exception giving 5 maple : 4 purple dotted non-maple. In F_2, in some cases, the browns bred true, in others only brown and colorless

resulted; while still others gave maples, browns, ghost maples and colorless.   One of the last type gave 20 maple: 6 brown: 5 ghost maple: 5 non-mapled.   Non-maple × non-maple segregates involving maple or ghost maple ancestry [Table 23 (86)] gave no maples in F_1.

Lock's (55) results are in general accord with Tschermak.

Maple × colorless gave in F_1, maple.   In F_2, 38 maple: 12 gray: 19 colorless were obtained, approximating a 9: 3: 4 ratio.   2 of the 19 colorless had ghost maple seeds, but there should have been a large proportion of these ghost maples.   Lock says ghost maple is for some reason almost unexpressed in this particular cross (maple × Victoria Marrow).

Crosses of F_3 offspring of all 19 colorless with either pure strains of gray or gray with purple dots (no maple) resulted in

7 colorless producing 17 maples: 15 non-mapled.
22 colorless producing all maples (over 50),
7 colorless producing all non-maple (over 26).

Colorless × gray, maple, purple spots gives in F_1 always gray with both mapling and purple spotting.   In F_2, Lock (55) obtained 11 gmp: 2 gm: 6 gp: 2 g: 4 white or colorless (one of which was ghost mapled).

In F_3, 467 offspring of these various classes were grown, none of which gave results in opposition to the interpretation of the genetics of seed coat colors given at the end of this review.

3 gmp F_2 plants gave:

	82 gmp:	20 gm:	21 gp:	9 g:	37	colorless
Ratio,	27	: 9	: 9	: 3	: 16	
Expected,	71.3	: 23.8	: 23.8	: 7.9	: 42.2	

4 gmp F_2 plants gave:

	75 gmp:	24 gm:	48 colorless
Ratio,	9	: 3	: 4
Expected,	81	: 27	: 36

F_4 whites derived from F_2 segregates of the cross just described were crossed with F_4 grays derived from the same source.

In F_5, 6 such crosses gave: 9 maples: 14 non-mapled,
  28 such crosses gave all maples (over 75),
  27 such crosses gave all non-maples (over 75).

Colorless × purple is only mentioned by Vilmorin (90), in which purple is said to be dominant.

Gray × gray, according to the data of Tschermak and Lock, may give only gray in F_1, F_2 and succeeding generations.

Gray × gray with purple dots, excluding exceptional cases such as are mentioned under colorless × gray with purple dots, always gives gray with purple dots in F_1 and grays with and without purple dots in F_2 in an approximate ratio of 3 : 1. The purple-dot pattern in the F_1 of both these crosses and those of colorless × gray with purple dots is much intensified, and in both cases the stippling pattern may vary so as to produce peas with wholly purple seed coats. These are found sometimes in pods containing some purple and some purple-specked seeds. In other cases a whole pod of a plant may contain all purple seed coat peas. Occasionally a seed may be half purple and half gray or maple. F_2 plants from seeds with purple seed coats do not give results differing from the purple stipple seeds. Bateson (1) thinks such purples are not present in pure stocks of purple-specked seed coat races, and that crossing in some manner promotes their appearance (see Darwin, Bateson, Lock, Tschermak, Fruwirth for further data on this subject). Fruwirth (34) experimented with the variety Blauhülsige, a purple-podded race of peas, which had in respect to seed coat color, four types of peas on the same plant, often mixed together in the same pod. These were either pure yellowish green, yellowish green with purple flecks or dots, purple with small greenish yellow flecks, and self purples, in respect to seed coat color. These are evidently degrees of variation of the same character. As they occur in a pure variety, Bateson's belief as to the effect of crossing as a stimulus to such extreme variation is not supported. Observed also by Lock on both pure and cross-bred strains (56).

Gray × gray with maple marbling gives in F_1 maple marbling, which in F_2 in simple crosses gives 3 maples: 1 gray. However, such simple crosses are rarely to be had and the crosses usually involve the purple-dotted pattern.

Gray with purple dots $\times$ gray with maple marbling gives in F_1 gray, purple-dotted, mapled seed coats. In F_2, Tschermak obtained 13 gpm : 13 gp : 12 gm : 2 g. From segregates similar in genetic composition to the F_1, Tschermak (86) secured

$$\text{in } F_3 — 29 \text{ gpm} : 9 \text{ gp} : 16 \text{ gm} : 6 \text{ g,}$$
$$\text{in } F_4 — 20 \text{ gpm} : 9 \text{ gp} : 12 \text{ gm} : 1 \text{ g,}$$

making in all three generations from F_1 plants or segregates of the same composition,

	62 gpm : 31 gp : 40 gm : 9 g
Expected,	79.8 gpm : 26.4 gp : 26.4 gm : 8.8 g
Ratio,	9 gpm : 3 gp : 3 gm : 1 g
Approximation,	6.9 gpm : 3.4 gp : 4.4 gm : 1 g

As maples and maples with purple dots are often hard to separate, the disproportion of gpm and gm may be due to this difficulty. 9 of the F_2 gpm were tested and in F_3:

1 gave all four classes,
1 gave gpm, gm, g (brown self),
4 gave gpm, gp, gm,
2 gave gpm, gp,
1 gave gm only, only one plant being grown.

Bateson (1) crossed gray with purple dots $\times$ maple (Irish Mummy). F_1 as given above and F_2 resulted in 4 classes, no ratios or numbers given. The 4 classes are brownish gray with purple dots, maple and purple dots, maple, gray and light purple specks. The first and last classes are probably the same, the difference resulting from environment. Great difficulty is experienced in discriminating between true browns and brown due to weathering.

Gray with purple dots $\times$ self purple gives in F_1, self purples (34). In F_2 these gave:

35 self violet or purple : 11 gray green, violet dots : 3 gray green.

The maternal parent of this cross had seeds varying on the same plant through all these classes. The paternal parent was a self-violet variety.

Vilmorin (90) also notes that self violet is a dominant to the various testa colors.

Brown hilum is always associated with colored flowers and apparently gives a simple 3:1 ratio in F_2, with dominance in F_1.

Black eye pattern, according to Correns (14), is both dominant and recessive in F_1 in crosses involving its presence and absence. Black-eyed Marrowfat × white-seeded Mummy (57.5) presumably gave only blackeye in F_1 and three classes of F_2 segregates—black eyed, sooty whites, and whites or colorless. Vilmorin (90) lists blackeye as a dominant. Blackeye is associated with both colorless and colored flowered and seed coat races.

Violet eye (86) × non-violet eye gives all violet eye in F_1. In F_2, Tschermak's crosses gave 53 violet eye:23 non-violet eye, a ratio of 2.3:1, approaching nearest to the 3:1 ratio. In F_3, all F_2 non-violet-eyed segregates tested, bred true. Two F_2 violet-eyed segregates in F_3 gave 7 violet eyed:6 non-violet eyed. Non-violet-eyed races crossed with non-violet-eyed segregates from violet-eyed and non-violet-eyed ancestry gave always non-violet-eyed progeny. Non-violet-eyed segregates from crosses involving violet eye always gave non-violet-eyed progeny. F_3 non-violet-eyed segregates × heterozygous F_3 violet-eyed segregate gave 5 violet-eyed:3 non-violet-eyed offspring. Total results obtained by adding together all progeny of heterozygous plants in Tschermak's data give 78 violet eyed:38 non-violet, or a ratio of about 2:1.

Violet eye, as is also presumably true of black eye, is not coupled in its inheritance with the substances which determine flower color, seed coat color, seed coat pattern and leaf axil color. Sufficient proof of this statement is given by Tschermak's (86) experiments.

All other seed coat patterns are associated in their inheritance in one way or another with the causes which determine the gray-brown colors of the seed coats, the color of the leaf axils, and flower color. Mapling, although a character inherited independently of the characters just enumerated, as shown by Tschermak and Lock, is largely dependent upon them for full expression. Purple spotting and gray are absolutely associated with these characters. Brown hilum color is also coupled with colored seed coats and colored flowers. Colorless seed coats, on the other hand, are always

associated with white flowers.   These various associations of the characters just mentioned, in their inheritance are, so far as our data go, *absolutely* without exception.

From the foregoing array of facts one may gather that the heredity of seed coat color is somewhat complicated as compared with that of other pea characters, but this is largely due to the ease with which such characters can be studied and consequently the amount of work that has been accomplished on them.

INTERPRETATION.

From a Mendelian standpoint, the heredity of seed coat color and pattern, as deduced from the foregoing mass of data, is comparatively simple.

Brownish, grayish green or gray seed coat color may be represented by the factor Gc which is absolutely coupled with the factor A for colored flowers.   In the absence of Gc, seed coats are colorless.   The factor J acts upon Gc so as to produce dark chocolate brown.   It is independent of Gc or A and is carried by either colored-flowered, gray seed coat varieties or white-flowered, colorless seed coat varieties.   In the latter, it remains without expression. The orange tint or color is regarded by Tschermak (86) as due to a factor H, which alters the gray color to orange-red or orange-yellow.   So far H has not been found in white-flowered races though there is reason to suspect its presence there (see p. 511). The factor U, which provisionally stands for self purple seed coats, is also probably coupled with A, although there are very little data on the subject.   Varieties with colored flowers then, carrying only the factor Gc, will have gray seed coats; if J is added, brown seed coats; if both J and H are added still brown seed coats, but if J is eliminated and only Gc and H are present, orange seed coats.   If the factor U for self purple is added to Gc, the seed coat is self purple.   No data are available as to other combinations of U.

Purple spotting is represented by Tschermak (86) as due to two factors, one coupled absolutely with A and Gc, the other independent, hence present in both white-flowered and colored-flowered varieties.   Lock (54, 55) represents similar results by one factor operating only in the presence of the factor for gray seed coat color.

Representing purple dotting by one factor simplifies the interpretation and amounts to the same thing as Tschermak's two factors since he regards one—the factor E—as absolutely coupled with Gc and A. The other factor (F) is inherited independently of Gc and A, hence may be present in either varieties with colored flowers and colored seed coats or in white-flowered varieties with colorless seed coats. As it expresses itself only in the presence of Gc, its presence in white-flowered races can only be determined by crosses with non-purple-dotted gray seed coat races. The exceptional cases noted above where purple-dotted seed coat fails to appear when expected, are interpreted by Tschermak (86) as due to lack of interaction between the factors F and Gc even though both are present. Non-purple-dotted seed coat races then may be either Gcf (Ef), gcf, gcF—the first colored flowered and the two latter with white flowers. GcF (EF) is, exclusive of the exceptional cases noted, always purple dotted.

Mapling is represented by one factor (54, 55, 86) M, which completely expresses itself only in the presence of Gc, but which may give a faint expression (ghost mapling) in gc white-flowered races. Exceptional cases similar to those found in connection with the inheritance of the purple dot pattern are interpreted by Tschermak (86) in the same way, namely the disassociation in the same plant of M and Gc. M is inherited independently of Gc, F, N and probably Pl.

Brown hilum color may be regarded simply as another expression of Gc since they are absolutely coupled.

Black eye and violet eye, so far as present data go, are to be regarded as due to the factors Pl and N, both of which are inherited independently of Gc, F, M, and of each other, and able to express themselves in either white- or colored-flowered races. The dominance of black eye over non-black eye in one cross and its recessiveness to non-black eye in another cross involving a different non-black-eyed variety is to be regarded as due to the interference of another factor or factors not yet delineated.

Data as to the relation of these various factors to each other in inheritance are still much to be desired, especially in the case of Pl, U, H and J. While Tschermak has done much toward throwing

light on seed coat color and pattern inheritance through making all sorts of crosses, back-crosses, reciprocal crosses and so on, his numbers in most cases have been lamentably small, consequently the approximation to the expected ratios on which the factor representations are based has not been close, and such ratios as 2:1 where 3:1 were expected are comparatively common.

The above interpretations account for practically all the experimental data on seed coat color in *Pisum*. There are no data, so far as I am aware, opposed to these interpretations, barring the smallness of the numbers by which the poor approximation to expected ratios is explained.

2. Cotyledon Color.

Varieties and species of *Pisum* as regards the cotyledon color of the ripe seed may be divided roughly into two classes—those with green cotyledons and those with yellow cotyledons. Between the extremes of these two classes, there are all gradations of cotyledon color from the darkest green through light green, yellowish green, green piebald with yellow spots, light yellow, bright yellow and dark orange yellow. Each of these classes is characteristic of a certain group of varieties, each variety possessing and breeding true to one of the above colors and to no other. Environment may alter the color generally characteristic of a variety so as to place it in another class. Some varieties are altered by common environmental changes much more than are others. Mendel (60), Hurst (42), Lock (55), Bateson (1), Darbishire (21), Tschermak (80, 81) and White (98) have all discussed this color variation in cotyledons both in relation to environment and to heredity.

Green Cotyledon.—Green cotyledon color varies from dark green in such varieties as Wisconsin Blue and Alaska to light green or yellowish green as is characteristic of Telephone, Blue Prussian and Duke of Albany. As first noted by Hurst (42) green wrinkled peas are always a shade lighter and tend to be more yellowish than the green smooth-seeded varieties. Varieties such as Scotch Beauty and other smooth-seeded dark greens do not fade to yellow upon exposure to moisture and light as easily as the wrinkled varieties or such smooth varieties as Express. Dark greens give the best results

in crosses with yellow cotyledon varieties if demonstration material for illustrating Mendel's law is desired. Lock found that green seeds exposed to light in a dry bottle for a length of time faded and became yellowish. Mendel and Tschermak both found that injury from the pea-weevil would produce yellowish blotches and even wholly yellow seeds. Such greens as Laxton's Alpha will always give some piebald and even some yellow seeds if the pods are left on the vines till they are all ripe (1). Piebald peas remain green if kept in the dark, and a dry place, but fade on the exposed surface on exposure to light. Piebald seeds of one pod are all tinged on the same surface. Tinged seeds of dark green types or varieties normally giving no piebalds are less viable than piebald peas of green-seeded varieties (1). Numerous selection experiments were made by Bateson (1) but tinged or piebald seeds produced no more seeds like themselves than did normal green seeds.

Telephone seed of all types retains its series of color gradations. Some varieties of peas such as Sutton's Nonpareil (1) are heterozygous for cotyledon color and of course these statements do not apply to them.

Yellow Cotyledon.—Yellow cotyledon color varies from light yellows and yellowish greens to deep orange-yellow, such as is characteristic of Späte Gold, and, as in the case of the greens, this color shading is a varietal characteristic, some varieties having light yellow peas and no other shade, *e. g.,* Goldkönig and *P. humile* of Sutton. The yellow color may remain somewhat greenish if the pods are not properly matured and certain varieties are extremely particular in this respect. Späte Gold is a dark green pea when immature but changes very rapidly to bright deep orange-yellow when mature. Even after the pods have the appearance of maturity and are dry, the change sometimes has not resulted. Improper maturing due to lack of sufficient light and in some cases to an over-supply of moisture is the usual cause of ununiform coloring in yellow peas. According to Bunyard (21, p. 131) both yellow and green cotyledon varieties have yellow and green pigment in their immature seeds, but the yellow cotyledon varieties possess an additional hereditary substance—an enzyme perhaps, which causes the green pigment to fade when the seeds mature. Green when present is

epistatic to yellow and thus masks it. Yellow cotyledon color is apparently the ancestral color of all our peas, as all the wild species of *Pisum* have only yellow cotyledons.

VARIETIES STUDIED.

No attempt will be made to give a list of all the varieties upon which genetic studies of cotyledon color have been made. Sufficient to say that at least a hundred are involved and these have been collected from all over the globe wherever peas are grown.

Orange Yellow to Yellow.

Très nain de Bretagne, Debarbieux, Sabre, Victoria Marrow, British Queen, Early Giant, Purple Sugar Pea—Bateson (1).

Ceylon Native Pea Nos. 1 and 2, Ringleader, French Sugar Pea —all Lock (54).

Purpurviolettschottigen Kneifelerbse, Bohnenerbse—Correns (14).

Grau Riesen, Désirat, various Svalöf *P. arv.* nos., Victoria, Couturier, Auvergne, Buchsbaum, Prince of Wales—Tschermak (79, 80, 81, 83).

Black-eyed Marrowfat, First of All, Späte Gold, Petit Pois, Wachs Schwert, Mummy, White Marrowfat, Elephanten, Abyssinian Black, *P. elatius,* Gold von Blöcksberg—White (98).

Light Yellow.

Goldkönig, *P. humile* ? of Sutton—White (98) ; Satisfaction— Lock (54).

Dark Green to Green.

Fillbasket, Express, Blue Peter—Bateson (1) ; Nonsuch, Earliest Blue, Eclipse—Lock (54) ; Grünen Erfurter Folger—Correns (14) ; Grünbl. Folger, Express, Greenseeded *P. sativum* of Svalöf, Serpette, Plein le Panier, Blue Peter, Fairbeard's Champion— Tschermak (79, 80, 81, 83).

Market Split Pea of New York City, Acacia, Velocity, Alaska, Scotch Beauty, Express, Nott's Excelsior, Laxtonian—White (98).

Piebald Greens.

Telephone, Telegraph—Lock (54); Telephone—Tschermak; Telephone, William I, American Wonder, Laxton's Alpha—Bateson (1); Telephone—White (98).

RESULTS FROM CROSSING.

Yellow $\times$ yellow always gives yellow in F_1 and succeeding generations, except in crosses with the light yellow cotyledon variety Goldkönig in which case a certain proportion of green cotyledon seeds are obtained in F_2, yellow being dominant in F_1. The ratio of yellows to greens in such crosses either approximates 3:1 or 13:3. The actual results (98) obtained from crosses of Goldkönig with four or five other yellows in F_2 were:

457 distinctly yellow:23 yellowish green:86 green.

Considering the last two groups together, the proportions are 457 yellow:109 green or a ratio of 13:3, the theoretically expected being 459.2 yellow:106.2 green. These peas were reclassified after mixing several times with the same result. No F_3 results have been obtained as yet.

Orange yellow $\times$ light yellow gives dominance in F_1 of the former (90).

Yellow $\times$ green gives all yellow in F_1 in all cases except where the variety Goldkönig is used. Where Goldkönig is used as a yellow, all F_1's are green. White (98) has tested out five different varieties with green cotyledons and always secured F_1 seeds of a distinct green color. Several cases of dominance of green were obtained by Lock (54), Tschermak and Bateson (1), but they are mostly explained by these experimenters themselves as either errors in labeling or in improper maturing. Repetitions of such crosses, using the same varieties, did not give these exceptional results.

In F_2, excluding Goldkönig from consideration, yellow $\times$ green gives yellows and greens again in the proportion 3 yellows:1 green. In F_3, all the greens breed true and give only green progeny. Of the yellows only about one third breed true to yellow, the other two thirds giving rise again to yellows and greens in the proportion of 3:1. The true breeding yellows and greens are believed to continue

breeding true, indefinitely, while the impure yellows in each generation continue to give rise to yellows and greens in the ratio of 3 : 1. Darbishire has followed this study through to the F_{11} or F_{12} generation and finds nothing to controvert this statement. The yellow and green seeds that came from such a cross appear to be the same sort of colors that the grandparental ancestors had. The tendency of yellows to be greenish because of immaturity, and of greens to fade is no more marked in the progeny than in their pure forbears.

The actual results from crossing pure yellow and green cotyledon plants are given in the following table :[3]

Hybrid Generation.	Observer.	Yellow.	Green.	Percentage of Green.
Second............	Mendel............	6,022	2,001	24.9
	Correns...........	1,394	453	24.5
	Tschermak........	3,580	1,190	24.9
	Bateson	11,903	3,903	24.7
	Hurst	1,310	445	25.4
	Lock.............	1,438	514	26.2
	Darbishire........	1,089	354	24.9
	White............	1,647	543	24.8
Third............	Correns...........	1,012	344	25.5
	Tschermak........	3,000	959	24.2
	Lock.............	3,082	1,008	24.6
	Darbishire........	5,662	1,856	24.7
Fourth............	Correns...........	225	70	23.7
	Lock.............	2,400	850	26.1
Total..........	58,254	43,764	14,490	24.9

Mendel (60) tested out 519 F_2 yellows by growing an F_3, the result being: 353 seeds gave yellow and green seeds (3 : 1), 166 seeds gave only yellow seeds, the ratio of the former to the latter being 2.13 : 1.

Darbishire (21) tested out in the same manner 140 F_2 yellows, which in F_3 gave: 98 F_2 seeds with both yellow and green progeny, 42 F_2 seeds with only yellow progeny, the proportions being 2.3 : 1.

Back-crosses (56) of F_1 or of similar heterozygous plants from later generations with the yellow parent gave all yellow as follows:

Mendel,   192 yellow : 0 green,
Tschermak, 126 yellow : 0 green.

[3] These data are taken from Darbishire (21) and White (98).

Heterozygous yellows or F_1's $\times$ the green-seeded parent gave a ratio of 1 yellow : 1 green as follows:

Mendel,   104 yellow : 104 green,
Tschermak, 101 yellow : 100 green.

As regards the F_2 generation from green $\times$ Goldkönig yellow, the data are as yet very scant. White (98), however, from an F_2 progeny of 14 crosses found 253 seeds had green cotyledons and 74 had yellow or yellowish with slight green tinge, the proportions approximating 3 green : 1 yellow or just the reverse of the common result. No F_3 generation data are as yet available. All green and yellow cotyledon varieties used in crosses with Goldkönig crossed with each other gave the usual 3 yellow : 1 green ratio.

In applying Mendel's law to data such as the above, one must always bear in mind, as pointed out recently by Pearl, that Mendelism is essentially a statistical method and the law a statistical deduction, requiring large numbers and dealing only in averages. The danger of drawing conclusions from small numbers is well shown in a survey of the extreme variation in F_2 ratios derived from single F_1 plants.

For example, the greatest variation in

Mendel's records (60) was 32 Y : 1 G and 20 Y : 19 G,
Bateson's records (1) was 60 Y : 9 G and 32 Y : 20 G,
Corren's records (14) was 92.3 per cent. Y : 7.7 per cent. G and
    55.8 per cent. Y : 44.2 per cent. G,
Lock's records (54) was 14 Y : 1 G and 7 Y : 8 G.

Bateson (1) conducted experimental inquiries to determine the significance of these fluctuations, but found them to be purely fortuitous, as did Mendel (60) before him.

INTERPRETATION.

In the light of the above data the hereditary differences between yellow cotyledon and green cotyledon varieties of peas may be designated by G and I. G represents the hereditary determining substances or factor for green pigment, while I is a factor or determiner which causes the green pigment to disappear when the seed

is mature. Y stands for yellow pigment and so far as known is common to all varieties of peas, whether green or yellow seeded. Green when present masks or covers up yellow pigment, hence is epistatic. The factor formulas for all varieties of peas so far genetically studied then are:

$$YYGGII = \text{true breeding yellow cotyledon races,}$$
$$YYggii = \text{Goldkönig (on the present data),}$$
$$YYGGii = \text{true breeding green cotyledon varieties.}$$

On the basis of these three formulas and by various combinations of these three types of varieties, all the various ratios described in preceding pages, as well as others, may be obtained. All genetic data, so far as I am aware, accord with this interpretation.

3. COTYLEDON FORM (SEED FORM) AND COMPOSITION

The seeds of peas as regards shape are either smooth round to roundish, or wrinkled and angular. The cotyledons of the seed are mainly responsible for these differences. Smooth, roundish peas, however, are often pitted or dimpled and this dimpling is of two types. One type is largely due to such environmental conditions as premature harvesting, while the other type remains pitted under practically all common environmental conditions. The latter type is designated " slightly wrinkled " by Tschermak and " indent " by the English geneticists. Indent, while a character which modifies the external appearance of the seed and cotyledon, belongs in reality to the generation preceding that to which the cotyledon characters—wrinkledness, color, etc., belong. Associated in inheritance with seed form are certain types of starch and certain germination, sugar content and color modifying characters, and because of this association they will all be considered under this heading. Indent peas and smooth peas will be treated separately.

Smooth round peas without indenting are most commonly characteristic of varieties with white flowers and colorless seed coats, although many varieties with colored flowers and colored seed coats have perfectly smooth seeds. Particularly is this true of most of the wild sorts, all of which have colored flowers. The starch grains of the smooth-seeded varieties according to Gregory (37), Darbi-

shire and others are simple, oval or potato-shaped and of large size
with well-marked hilum centers and distinct lines of stratification.
Darbishire (19), and Kappert (48) found small round grains asso-
ciated with the larger oval ones, and occasionally these are divided
by a single split or fissure which cannot be increased in size through
the action of diastase and ptyalin (48). Kappert (48) also has
observed these longitudinal fissures with short side splits occasionally
among the large oval grains. The size of the starch grains vary
considerably in different cell layers of the same seed, the smallest
being found in the outer layers, where the protoplasm is most dense.
Measurements of starch grains, given in the following table, show a
considerable variation, though the data are too scant to be of much
weight.

Investigator.	Variety.	Ave. Length.	Ave. Breadth.	No Grains Measured.
Gregory........	Several varieties	.06–.34 mm.		
Darbishire......	Eclipse	–.0322 mm.	.0213 mm.	232
Kappert........	Laxton's Vorbote	–.0363 mm.	.0246 mm.	50

Darbishire divides the length by the breadth $\times$ 100 and secures
the breadth-length index (in Eclipse 66.14) or the breadth in terms
of per cent. of length. The breadth-length index for Laxton's
Vorbote is 67.8–69.1 and for Emerald Gem starch grains 74.3 (48),
indicating that starch grains of some smooth-seeded varieties are
less oval than others. The long oval starch grains are characteristic
of the early as well as of the late stages of seed development.

According to Denaiffe (23), Halsted, Darbishire (19), Kappert
(48) and others, round smooth peas take up less water upon ger-
mination than wrinkled peas. Darbishire found the average absorp-
tive capacity (or the amount of water an immersed dry pea would
take up in twenty-four hours, expressed as percentage of weight of
the dry pea) of 12 Eclipse peas to be 86 per cent. Kappert found as
regards absorptive capacity so much variation in the seeds even
of the same sort on the same plants that he regards the methods
used by Denaiffe and Darbishire as extremely inexact. Kappert
gives the water loss of air dry seeds of smooth-seeded peas in

terms of per cent. of green (fresh) seed weight.   For the following varieties this is:

        Laxton's Vorbote .... 5 seeds .... 44–58.21 per cent. loss.
        Emerald Gem .... 6 seeds .... 44–58.66 per cent. loss.
        Carter's First Crop .... 4 seeds .... 40–54.87 per cent. loss.

He considers the variation in water loss between seeds of the same sort or variety as due in part, at least, to differences in environment.   Chemical analysis of air dry peas of 2 different varieties of smooth seeded peas—Carter's First Crop and Bohnenerbse—showed a water content of from 10 to 12 per cent. or from 1–2 per cent. more water than in similar analyses of wrinkled peas.   In fresh green seeds the difference in water content amounts to as much as 8 per cent. more in wrinkled than in smooth seeds.   Chemical analyses show also that smooth-seeded peas possess a relatively small amount of water and alcohol soluble material.   Difference in sugar content between the two types, however, is small (.7 to 3.4 per cent.) varying in smooth-seeded peas from 1.96 to 3.29 per cent.   There appears to be about twice as much sugar and dextrine in dry wrinkled peas as in dry smooth peas.   Smooth round seeds appear to always have deeper colored cotyledons than wrinkled peas.

Indent peas are known to differ from smooth round peas only in being indented.   Both the cotyledon and the seed coat are affected and the characteristic only appears on peas with colored seed coats and colored flowers.   The starch grains are indistinguishable (37, 1).

Wrinkled, angular peas differ from indent and smooth round peas in at least four characters, *viz.,* the shape and surface of the seed, the shape and constitution of the starch grain, the water content of the leaves and green immature seeds and the sugar content. Seeds of smooth-seeded varieties are sometimes unclassifiable because of pitting, but, so far as I am aware, seeds of wrinkled seeded varieties never vary toward greater smoothness (barring sports and rogues).   Wrinkling is always associated with round compound starch grains.   These starch grains are made up of from two to eight

or more divisions or separate irregularly shaped small particles cemented together by a yellowish substance which is not colored blue by iodine (19). The most common grains are 4–6-particled. Both Kappert (48) and Darbishire (19) occasionally found potato-shaped grains similar to those of round-seeded peas among the compound starch grains. Small round grains are always present. Kappert (48) found the starch grains of very young peas (2–3 weeks old) to be free from splitting, and through observations on later stages, he found all gradations from simple round grains to the characteristic compound or radially split grain of 2 to 8 particles. This led him to conclude that compound starch grains are simply radially split simple starch grains and with only one starch formation center instead of 2 to 8 such centers as is commonly supposed. The so-called compound grains may be further broken up through the action of diastase and this led Kappert to believe the starch of wrinkled peas was more soluble than that of smooth-seeded peas, a supposition made more plausible through the greater amount of sugar and dextrine present.

Both Gregory (37) and Darbishire (19) found the compound starch grains of the wrinkled peas they studied to be smaller than the starch grains of smooth-seeded peas.

The data from measurements of several varieties are given below:

Investigator.	Variety.	Diameter.	No. Grains Measured.
Gregory (37)........	Several	.06–.2 mm.	...
Darbishire (19)......	British Queen	.0248–.0269 mm.	105
Kappert (48)........	Goldkönig.........	.0245–.0268 mm.	20

The breadth-length index for starch grains of wrinkled peas of course is higher being 92.2 for British Queen and 91.5 for Goldkönig.

Denaiffe (23), Darbishire (19), Kappert (48) and others all agree that more water is taken up by dry wrinkled peas than by smooth peas. Chemical analyses as given by Kappert show that the water content of the air dry smooth and wrinkled peas differs only by 1 or 2 per cent. in favor of the former. However, fresh wrinkled peas before they are ripe are said to have possibly as high as 8 per

cent. more water than smooth peas, and it is largely because of this greater water loss that the wrinkled condition of the cotyledons and seed coat is brought about and not because of difference in sugar content as contended by Darbishire (19). Difference in sugar content from the writer's knowledge of pea varieties, is probably very variable. Correlated with the larger water content of unripe wrinkled peas is a larger water content of their leaves as compared with leaves of smooth seeded varieties.

Seed of wrinkled varieties of peas as compared with smooth seeded peas, usually lose their power of germination and rot more quickly under unfavorable conditions, such as cold, wet weather. Wrinkled peas are a shade lighter in cotyledon color than smooth peas from the same pod or plant and grown under the same environmental conditions.

Varieties Studied.

Because of the large number of genetic experiments on these characters, only a partial list of the varieties studied can be given.

Smooth Round.

Eclipse, Genoa round, *P. arv. hibernicum,* Bohnenerbse, Sangster's No. 1 (?)—Darbishire (19).

Express, Fillbasket, Très nain de Bretagne, Carter's Telegraph, Victoria Marrow, Maple—Gregory (37).

Express, Très nain de Bretagne, Victoria Marrow, Blue Peter, Fillbasket—Bateson & Kilby (1).

Ceylon Native No. 1, Ringleader, Ceylon Native No. 2, Sutton's Telegraph (?)—Lock (54).

Laxton's Vorbote, Emerald Gem, Carter's First Crop—Kappert (48).

Harrison's Early Eclipse—Hurst (42).

Emerald, Yellow Pod Sugar Pea and numerous others—Tschermak.

Over 20 varieties (unpublished data)—White.

Indent.

Purple fl. Field Pea, Purple Sugar Pea, Sutton's Purple Podded Pea —Gregory (37).

Purple Sugar Pea, Graue Riesen—Bateson & Kilby (1).
Graue Riesen, Svalöf *P. arv.* No. IV., and No. X.—Tschermak (86).
Irish Mummy, Gray Sugar and others (unpublished data)—White.

Wrinkled, Angular.

British Queen, Laxton's Alpha, Telephone—Darbishire (19).
William I. ?, Telephone, Laxton's Alpha, Serpette nain blanc, Dark
   Jubilee, Early Giant, British Queen, Windsor Castle—Gregory
   (37).
Laxton's Alpha, Serpette nain blanc, Telephone, Veitch's Perfec-
   tion—Bateson & Kilby (1).
Telephone, Satisfaction, Nonsuch, British Queen—Lock· (54).
William Hurst, Laxton's Alpha, Goldkönig—Kappert (48).
British Queen—Hurst (42).
Prince of Wales, Telephone and others—Tschermak.
Goldkönig, Quite Content, Nott's Excelsior, Laxtonian, and many
   others—(unpublished data) White.

RESULTS FROM CROSSING.

Round smooth, white flowers × round smooth, white flowers
always gives round smooth seeds and white flowers in F_1 and suc-
ceeding generations.

Round smooth, white flowers × round smooth, colored flowers
in F_1 (of cotyledons) gives round smooth seeds,, but in F_1 of seed
coats (F_2 of cotyledons) gives all indent seeds. In F_2 of seed coats
(F_3 of cotyledons) the number of F_2 plants bearing all indent seeds
to those with only smooth seeds approximates $9:7$. The *reciprocal*
of this cross in F_1 (of cotyledons) as well as in F_1 of seed coats
(F_2 of cotyledons) gives all indent seeds, while in F_2 the results are
the same as when the white-flowered smooth-seeded variety is used
as the maternal parent.

According to Tschermak (80, 81, 86), Lock (54), Bateson (3)
and others who have experimented with indent varieties, the indent
seeds are always borne on plants with colored flowers and there has
never been an exception to this association recorded. According
to the same observers, white-flowered plants in such crosses always
have smooth and never indent seeds. Plants with colored flowers,

however, often have smooth seeds and it is to be inferred from Tschermak's data and formulas (86) that in crosses of round smooth, white flowers with round smooth, colored flowers, the F_2 generation consists of three classes—indent, colored flowers; round smooth, colored flowers; round smooth, white flowers. As regards the seed characters, only two classes are present—indent and smooth. From crosses of four round-seeded, colored-flower varieties with five round-seeded, white-flowered varieties, Tschermak (86) secured in F_2:

$$181 \text{ indent} : 96 \text{ smooth or } 1.89 : 1.$$

In F_3 part of the indent and part of the smooth seeds bred true, while a part of each class again gave both indent and smooth seeds. From this and other data of Tschermak's one may consider the above F_2 numbers as a very poor approximation to a $9 : 7$ ratio— the actual results expected had the approximation been perfect being 155.7 indent : 121.1 smooth.

Round smooth, white flowers $\times$ indent, colored flowers in F_1 (of cotyledons) always gives round smooth seeds, while the F_1 of the reciprocal cross, where the maternal parent has colored flowers, consists of indent seeds (Tschermak 80, 81), [(Correns), Bateson 3]. The F_1 of seed coats (F_2 of cotyledons) consists entirely of indent seeds and colored flowers, while in F_2 of seed coats (F_3 of cotyledons) indents and colored flowers to round smooth and white flowers occur in a ratio approximating 3 indent : 1 round smooth. The above description of the facts applies to all but one cross of this type. In this exceptional case, the round smooth white-flowered Nain de Bretagne was the pollen parent in a cross with an indent variety. The F_1 was indent, as usual, but the F_1 of seed coats (F_2 of cotyledons), instead of giving all indent seeds, as is commonly the case, gave quite definitely indents and rounds in the ratio of 3 : 1. Three such F_1 plants gave 339 indent, 119 round smooth, and 39 uncertain or of an intermediate type. Further, one F_2 plant apparently grown from the round seeds had only round seeds with colored seed coats (F_2 of seed coats, F_3 of cotyledons) (Bateson 3, p. 262).

Round smooth, white flowers $\times$ wrinkled, white flowers give in F_1 (of cotyledons), all round smooth seeds, which in F_2 give ap-

proximately 3 round smooth: 1 wrinkled. There is no case of coupling known between these two cotyledon characters and flower color, so the ratio is 3:1 whether the flowers are white or colored. In F_3 about one third of the round seeds produce only plants having round seeds, while two thirds of the round seeds again produce plants which have round seeds and wrinkled seeds in the proportion of 3:1. The wrinkled seeds always breed true. The results from crossing round smooth and wrinkled seeded varieties as obtained by five well-known geneticists are:

Hybrid Generation.	Investigator.	Round.	Wrinkled.	Per Cent. of Wrinkled.
F_2...............	Mendel	5,474	1,850	25.2
	Tschermak	884	288	24.6
	Bateson	10,793	3,542	24.8
	Hurst................	1,335	420	23.9
	Lock.................	620	197	24.1
F_3.............	Tschermak	2,087	661	24.0
	Lock.................	769	259	25.2
F_4.............	Lock.................	2,328	812	25.8
Total........	32,319	24,290	8,029	24.85

Back-crossing heterozygote F_1 with pure round smooth parent gave:

	Round.	Wrinkled.
Mendel	192	——
Tschermak	38	——

Back-crossing heterozygote F_1 with pure wrinkled seeded parent gave round smooth and wrinkleds in the ratio of 1:1 or

	Round.	Wrinkled.
Mendel	106	102
Tschermak	26	18
	132	120

No coupling or "correlation" of other common characters such as tallness, flower color, cotyledon color, fasciation and pod color with wrinkledness have been recorded. Partial coupling between wrinkledness and lack of tendrils ("acacia") has been studied by Vilmorin (88, 89), Bateson (88) and Pellew (64). This will be discussed in connection with foliage characters.

Darbishire (19) regards the shape and constitution of the starch grain, the water absorptive capacity of the seed and the shape of seed (round, smooth or wrinkled) as four separately inherited characters. This deduction is based on a series of observations on crosses of round and wrinkled varieties which demonstrated the F_1 nature of the starch grains, as regards shape and constitution, and the water absorptive capacity of the seeds to be intermediate between the two parents used. Although round smooth, the F_1 seeds had about equal proportions of simple and compound starch grains — and the latter instead of having on the average 6 particles per single grain as in the wrinkled parent averaged only 3 particles. Five seeds each of 48 F_4 plants were used instead of F_2 seeds for determining segregation phenomena. Sixteen plants were pure round-seeded segregates and had starch grains of the ancestral round parent type. Twenty plants were heterozygotes and had pure round, heterozygote round and wrinkled seeds. Only the round seeds were examined. Out of each of the 20 lots of 5 seeds, at least one had starch grains similar to the F_1 and in several cases all were similar to the F_1 seeds as regards shape and degree of compoundness. The homozygote rounds were easily distinguished from the other rounds. The heterozygote round seeds, while either roundish or irregular in shape, varied greatly in the proportion of compound to simple grains they possessed. In 2 cases, where countings were made, one gave 203 compound and 305 simple, while the other had only 28 compound out of 304 counted. The degree of compoundness of the starch grains varied in different seeds, some being many particled and some seeds with only few-particled grains. No progeny test of the correctness of the determination of homozygous and heterozygous rounds by observation of their starch was made, but the results were checked up by the approximation to the ratio of 2 heterozygote: 1 homozygote seed. The 12 plants with wrinkled seeds had the wrinkled ancestor type of starch grain, except in two or three seeds out of 45 examined, in which a few simple grains were observed.

As regards water absorptive capacity, F_2 peas with round compound starch grains and F_2 peas with long simple grains both had the same absorptive capacity as the F_1 pea with both kinds of starch

grains. From these facts, Darbishire holds the intermediate nature of the F_1 starch grains is not responsible for the intermediate absorptive capacity of the F_1 seed. High and low absorptive capacity is to be regarded as a separate pair of characters. Darbishire has not shown, however, that wrinkled F_2 seeds differ markedly in absorptive capacity, which should be the case, unless the character of the wrinkled pea completely masks any such difference in absorptive capacity.

Kappert (48), working over the same problems, secured results only partially agreeing with those of Darbishire. He agrees with Darbishire as to the intermediateness in form and constitution of the starch grains and the absorptive capacity of the F_1 seeds. He also finds great variation in absorptive capacity of the F_2 round seeds, but offers a choice between two explanations—differences in environmental influences during development owing perhaps to position of seed in the pod, or Darbishire's interpretation. Kappert finds this variation in water absorptive capacity true of round peas in the same pod in pure round-seeded varieties as well as in round-seed segregates, and this is true when only seeds of same size, weight, etc., are considered. Denaiffe, Darbishire and Kappert all agree that wrinkled seeds in general have a higher water absorptive capacity than round smooth peas, and hence there must be a close correlation of some sort between the character of the starch and ability to take up water. Both Darbishire and Kappert found the water absorptive capacity of F_1 peas to be nearer that of the round smooth parent, while the starch grains should be considered as more nearly approaching the wrinkled type, except in Kappert's crosses involving " Laxton's Vorbote " (round smooth) and " Goldkönig " (wrinkled). In these crosses, the F_1 starch was very similar to " Laxton's Vorbote."

Kappert finds no grounds for Darbishire's statement that both simple and compound starch grains are found in about equal proportions in F_1 seeds, but thinks the starch grains Darbishire took for simple were split on the narrow side, which Darbishire would have noted if he had turned them over, as Kappert himself has done repeatedly. Splitting of starch grains, according to Kappert, may take place fortuitously and not necessarily because of an inherent

tendency to split up, and both these influences may be operating in the seeds of the same cross. As regards shape and constitution of the starch grains in the hybrid seeds, Kappert secured distinctly different results depending on the round smooth parent used. Laxton's Vorbote and Goldkönig gave starch grains approaching those of the round smooth seeded parent, while Emerald Gem (round smooth) and Goldkönig gave *round, radially* split starch grains in large numbers, though the splitting was much less than in pure Goldkönig starch. Further, in F_2 Kappert was not able through microscopic examination of the starch grains to separate with certainty the homozygous rounds and the heterozygous rounds. Seeds of the same pod (all round) gave a continuous series of seeds with clearly intermediate starch grains to seeds with only simple starch grains. From the camera-lucida drawings of F_2 round seeds from two pods, one from each cross as noted above, those having Laxton's Vorbote as the round ancestor differed considerably in extent of split or compound grains from those with Emerald Gem as the round-seeded ancestor, leading the writer to believe in genetic differences between the round seed varieties. Kappert himself is uncertain as to whether the continuous gradation in extent of splitting results from hereditary or environmental differences.

Round smooth, colored flowers × round smooth, colored flowers always gives in F_1 all round smooth and colored flowers and from unpublished data of my own, only round smooth are present in later generations. Bateson (3, p. 263), citing Tschermak (81, p. 30, case 9), mentions an exception to this statement. The case cited is Tschermak's cross *P. arv., VI.* (round) × *P. arv., IX.* (round)? which gave *distinctly* dimpled seeds in F_1 of seed coats (F_2 of cotyledons). Tschermak's description in the same paper of the seeds of *P. arv., IX.*, is " roundish, rarely few dimpled seeds," indicating that there may be some doubt as to whether the *P. arv., IX.*, parent used was not indent instead of round. In later publications (86, see formula for *P. arv., IX.*) he describes this variety as definitely round-seeded. In another place in the same paper (81) devoted to assembled results, the crossing of two smooth-seeded *P. arv.* varieties is stated to always give smooth-seeded offspring in the first seed generation, which I take to be F_1 of seed coats (F_2 of

cotyledons and of Bateson). Tschermak, so far as the writer can discover, makes no mention of the results of this cross as exceptional.

Round smooth, colored flowers × wrinkled, white flowers in F_1 (of cotyledons) is indent, which in F_2 of cotyledons (F_1 of seed coat) give approximately 3 dimpled: 1 wrinkled (54). According to Lock, dimpled and wrinkled seeds are very hard to distinguish, as of course true wrinkling occurs in colored seed coats.

Indent × indent (colored flowers always) gives in F_1 and later generations always indent and colored flowers.

Indent × wrinkled, white flowers in F_1 gives indent. Reciprocal in F_1 (of cotyledons) gives round smooth seeds. In F_2 (F_1 of seed coats) of both crosses, indents to wrinkles appear in a ratio of 3 : 1 and the plants all have colored flowers.

The wrinkled seeds when sown give 3 wrinkled with colored flowers: 1 wrinkled with white flowers. The indent seeds if sown [(F_2 of seed coats) F_3 of cotyledons] likewise give rise to 3 colored-flowered plants: 1 white-flowered plant. The colored-flowered plants have either all indent seeds or indent and wrinkled seeds in the ratio of 3 : 1. The white-flowered plants have either all round seeds or 3 round: 1 wrinkled.

Indent × wrinkled, colored flowers. No data.

Wrinkled, white flowers × wrinkled, white flowers always gives wrinkled seeds and white-flowered progeny.

Wrinkled, colored flowers × itself. No data.

Back crosses (81) of various combinations involving indent ancestry gave no exceptional results, as viewed from the interpretation given for all the crossing data.

INTERPRETATION.

The preceding data concern two sets of characters—(1) round smooth cotyledons of low water absorptive capacity with simple, long starch grains and angular wrinkled cotyledons of high water absorptive capacity with radially split (compound), round starch grains; (2) indent and non-indent seeds. In the first set, round smooth and the characters associated with it are to be regarded as the expressions of a factor R, in the absence of which the cotyledons

are angular, wrinkled, etc.   The partial dominance of shape and constitution of the simple long starch grains in F_1 is perhaps modified by other factors not yet determined or due to the presence of R in simplex condition.   It is very evident from the diverse results of Darbishire and Kappert as regards F_1 starch characters that dominance of the simple or the " compound " type is inhibited in one case at least.

So far as is known, the factor R is inherited independently of all other *Pisum* factors excepting the factor for tendrils (Tl) with which it is partially coupled.   Interpreted as above, round-seeded varieties of peas have the formula RR while wrinkled varieties have the formula rr.

Indenting in peas, as interpreted by Tschermak, Bateson, Lock and others, is due to two or three (?) pairs of factors, one of which is the pigment-producing factor A, which gives rise to pink flowers and gray seed coats.   Indent peas only occur on plants with colored flowers, all of which have the factor A.   A may be substituted for Tschermak's factor L_1 since L_1 and A are *always* associated.   Taken thus the real indenting factor may be designated as L_2, in the absence of which in plants with colored flowers, the seeds are non-indent.   When A and L_2 are both present the flowers and seed coats are colored and the seeds are indent.   When A is absent but L_2 present, the flowers and seed coats are white or colorless and the seeds non-indent.

Thus all varieties of peas so far experimented with, having colored flowers, colored seed coats and indent seeds, may be represented by the formula AAL_2L_2, those with colored flowers, colored seed coats and *non-indent* seeds by AAl_2l_2 and those with white flowers, colorless seed coats and non-indent seeds by aaL_2L_2, because the latter in crosses with colored-flowered, non-indent types give in F_1 (of seed coats) all indent peas.

Considering the two sets of characters together, the factor A is found to mask the factor R or is epistatic, to use Bateson's term. The absence of R, *i. e.,* r or wrinkledness, on the other hand is epistatic to A.   The varieties of peas thus far genetically studied on the basis of the interpretation given above, fall into four classes which are

Round smooth, colored flowers $= AAl_2l_2RR$,
Round smooth, white flowers $= aaL_2L_2RR$,
Indent, colored flowers $= AAL_2L_2RR$,
Wrinkled, white flowers $= aaL_2L_2rr$.

Excepting the two exceptional cases mentioned under crossing results, all the data are in conformity with the interpretation and the formulas given, and the various results given from crossing may all be obtained through combinations of these four genetic types of varieties. The two exceptional cases need further confirmation, as one at least is doubtful as to fact.

Satisfaction is the only wrinkled pea with the aaL_2L_2rr formula so far studied, while the other varieties are numerously represented in the studies of Bateson, and Tschermak. Tschermak (86) gives the formulas for seven smooth round or indent with colored flowers and five smooth round, white flowered varieties with which he experimented. In his formulas, A and L_1 are separate factors, but since they appear always to be associated it is simpler to regard them as one.

4. SEED SHAPE.

Though only slightly studied, except as regards the two or more factors controling cotyledon shape (round smooth, angular wrinkled, indent), seed shape is known to be determined in part by still other sets of factors, which are not associated with those of cotyledon form and indent. Hurst (42) suggests that angularity, squareness, flattened sides (flat peas) and deep dents on the sides (not indent) are directly determined by the pressure of the peas of a pod against one another and by the constriction of the pod itself. Generally speaking, he thinks the roundest peas have plenty of room in the pod, while the most wrinkled angular peas are tightly packed together. Irregularity in shape may be caused by a struggle for growth room among the peas of the same pod, and thus alter their hereditary tendency to roundness. Lock (54) in the F_2 of certain crosses between varieties with narrow pods and round seeds and varieties with wide pods and flat seeds, found as a rule that flattened seeds were associated with wide pods and cubical or spherical seeds with narrow pods. In exceptional cases, wide pods had round or

cubical seeds and when an F_3 from them was grown, both wide and narrow pods were obtained, thus showing them to be heterozygous for pod width.

Observations of my own on over two hundred varieties, and crosses between several of them, in general, confirm Lock's observation as to the association of round or cubical peas with narrow pods and flat (whether angular wrinkled, or roundish angular and smooth) with wide pods. The diameter of the pod, however, is not necessarily to be regarded as a character which modifies the expression of the factors for seed shape, since it can well be that some of the factors which determine seed shape are coupled or partially coupled with those determining pod diameter. In the former case the seed and pod characters under discussion would be regarded simply as different expressions of the same factor. Wrinkled peas are practically always flat or cubical, but smooth peas may be cubical with rounded edges (drum-shaped), bean shaped, flat and rectangular with rounded corners, conical (if end pea in the pod) and spherical. Bean-shaped peas are characteristic of one variety (Bohnenerbse of Haage & Schmidt), but occasionally a single typical bean-shaped seed appears among a crop of round seeds. When planted, only round seeds are produced, so the variation, in the latter case, is largely due to special environmental conditions of some sort.

5. Seed Dimension and Weight.

These two characters are mutually dependent upon each other. Greater size generally means increased weight, though not necessarily so, especially when the composition of the seed, either chemical or morphological, is altered. Both round and wrinkled pea varieties have large and small seeds. The smallest seeds are found in some of the western Chinese varieties introduced into the United States by our Department of Agriculture, though several of the wild species have seeds of about the same size. The so-called wild *P. arvense* types of Europe and several forms of *P. elatius* have comparatively large seeds. Some of the largest seeded pea varieties are French Giant Gray Sugar, Champion of England, White-eyed Marrowfat, and Black-eyed Marrowfat. As compared with the latter,

the wild *P. elatius* seeds are intermediate in size between them and the small Chinese peas and such wild peas as *P. humile* and *P. quadratum*. Size and weight of pea is to some extent associated with size of plant and pods, though small dwarf plants such as Laxtonian bear relatively large pods and seeds. Delicate-stemmed plants such as Benton, *P. quadratum, P. humile,* Abyssinian Black, *P. Jomardi,* Velocity, Express and many of the Hindu and Chinese varieties do not bear large seeds or large pods. Pods and seeds of small, intermediate or of large size may be associated with tall or large, robust-stemmed plants.

In crosses, Bateson (1) finds that small and large seeds generally give intermediates in F_1 and F_2, although he has seen one cross suggesting segregation. Macoun (57.5) crossed two peas of about equal size (Black-eyed Marrowfat and White-flowered Mummy) and in F_2 secured the parental types and intermediates as well as seeds very much smaller than any of the common cultivated varieties. The latter bred comparatively true in F_3. Vilmorin (90) states large size of seed to be dominant to small size. Tschermak (81, 86) has gone into the subject with customary Teutonic thoroughness, but has published his results only in part. In general, he finds the F_1 generation of large × small seed to have seeds of intermediate weight, though nearer in weight to the small-seeded parent. In F_2, a continuous series between the two parents was obtained, with a great scarcity of the two grandparental types. Repeated experiments with large numbers always gave the same results, though in a few cases seeds still smaller than those of the small-seeded grandparent appeared. In F_3, at least one of the F_2 intermediates remained constant.

In back-crosses of the F_1 with the small parent, the F_1 seeds were small to possibly still smaller than the small parent, while the same F_1 back-crossed with the large-seeded parent gave intermediates, occasionally some seeds of which were larger than the F_1 of (large × small) itself.

As an illustration of his actual results, large *P. sat.* (ave. wght. 0.3305 gm.)× small *P. arv.* (ave. wght. 0.08649) in F_1 gave intermediates, ave. wght. 0.1648 gm., which in F_2 gave a continuous series which Tschermak classified in 4 groups—those with seeds averaging

in weight that of the small grandparent (I.), of the large grandparent (IV.) and those with seeds weighing on the average either more (III.) or less (II.) than the average weight of the F_1 seeds. The F_2 results from about 12 F_1 plants were:

I.	II.	III.	IV.	Total.
10	398 + 10 ?	105 + 10 ?	2	525
12	205	53	1	271
22	603 + 10 ?	158 + 10 ?	3	796

The F_2 progenies of the 12 or more F_1 plants were similar in composition, only those with the largest numbers giving the extreme variants. It is not clear as to whether parents, F_1's, and F_2's were grown under the same conditions, and in one case at least the F_1's and F_2's appear to have been obtained in different years. In my own experiments, seed size is quite sensitive to environmental differences, peas of the same pure line being almost twice as large under certain conditions than under others. The effect of environmental changes also varies with different varieties.

In crosses between large- and small-seeded varieties made at the Brooklyn Botanic Garden, the F_1 generation generally has as large seeds as the large-seeded parent, while crosses of large seed × intermediate (true breeding) seed has given in F_1 intermediates. In studies of such a character as seed size or weight, which has so many true breeding variations, a marked difference in results from crossing of different varieties is to be looked for, and while some of these crosses should give simple results, in other cases results of the most complex character are to be expected.

INTERPRETATION.

Crossing data on this character are too scanty to give much time to interpretation. Tschermak (86), while not definitely committing himself, is inclined to interpret his results as due to several factors, possibly four, though by combining groups I., II. and III., IV., a ratio varying from 3.5 : 1 to 4 : 1 is secured. One of the many objections to considering seed weight to be determined by the presence or absence of a single factor is the breeding true in F_3

of some of the F_2 intermediates. On the four-factor interpretation, the extreme scarcity in F_2 of the large-seeded grandparental type is accounted for by regarding its factorial composition as due to all four factors in a homozygous condition (AABBCCDD). Combining the F_2 classes I., II. and III., the F_2 ratio of small and intermediate seed weights to large seed weight is 793 : 3 or 264 : 1 which is somewhat close to the theoretically expected ratio (255 : 1). Likewise the relation of the small-seeded F_2's to the remainder of the F_2 progeny on a four-factor basis is theoretically 7 : 248 : 1, while Tschermak's actual numbers were 22 : 771 : 3 or 7.3 : 257 : 1. According to his provisional hypothesis, the 22 small-seeded F_2's represent not only those which will breed true (aabbccdd) but also small-seeded forms which will give intermediates (aabbccDd, aabbCcdd, etc.). Tschermak finds no evidence in his experiments for believing that sterility is in any way responsible for the small F_2 numbers of the large-seeded segregates. He also finds no reason for believing in a differential relation of the environment which would be so much more unfavorable to the large-seeded types.

6. HEIGHT, STEM DIAMETER, INTERNODE LENGTH AND INTERNODE NUMBER.

As described by Mendel and most geneticists since 1900, the heredity of height or length of stem in peas represents a very simple problem, the presence and absence of a factor for tallness. While Mendel's description and interpretation of results from crossing talls and dwarfs accounts for most of the facts derived from studying the genetics of two varieties differing in height, it fails to account for all the facts when pea varieties in general or as a whole are under consideration. Height in peas is generally arbitrarily divided into dwarfs (23–90 cm.), half drawfs (90–150 cm.) and talls (150–300 cm.). As pointed out by Lock, Keeble and others, height of a given variety in any given year is very much influenced by environmental conditions, so that in any detailed study of the heredity of height, parents, F_1 and subsequent generations should be grown side by side, as this method insures a minimum amount of variation in the environment. The environmental conditions which modify height are numerous, including defective or

diseased cotyledons, partially successful attacks of strangling fungi, temperature and humidity variation, lack of sunlight, variation in soil richness, etc. Dwarfing of tall varieties may be brought about and the flowering period delayed as much as three weeks (26) by cutting off part of the cotyledon in germinating peas. Lock (54) found the climate of Perideniya directly modified the height and growth habit of various varieties of English peas with which he experimented. Further the difference between the height characters of the Ceylon-grown English peas and the same varieties grown in England remained constant through five generations. At the Brooklyn Botanic Garden, Black Abyssinian peas when grown in the field plots bloom early and reach a height of never more than 60 cm. while under greenhouse conditions in the winter time under a temperature of 48° F.–55° F. and growing two plants per 10 cm. pot, they reach a height of over 120 cm.

Height is best described in terms of internode length and number, and stem diameter, as in reality the length of a plant stem is due to various combinations of these three elements. Described by this method, and only taking into consideration height in peas under the general climatic and soil conditions of Long Island, it appears best to modify the height ranges assigned to talls, half dwarfs and dwarfs as given by Bateson (1) and Keeble (49).

Tall peas (150–360 cm.) have robust stems made up of a large number (40–60) of short internodes or a much lesser number (20–47) of long internodes. This class also has very long roots (1).

Half-dwarfs (60–150 cm.) have either robust or delicate stems made up of a small number (10–24) of long internodes or a larger number (20–40) of short internodes. This class is very unsatisfactory, as it represents a very large number of diverse intermediate types.

Dwarfs (23–60 cm.) have either robust or delicate stems made up of a comparatively small number (8–18) of short internodes. This group is easily and accurately distinguished from either of the above, even in young stages 3 weeks or so old.

<center>VARIETIES STUDIED.</center>

<center>*Talls.*</center>

Purple Sugar Pea, Victoria, Laxton's Alpha and others—Bateson
(1).

British Queen—Hurst (42).

Telegraph, Ceylon Native No. 1, Telephone, French Sugar Pea—
Lock (54).

Numerous varieties—Tschermak.

French Sugar, Market Split Pea, Wachs Schwert, *Pisum elatius,*
Mummy and others—White (unpublished data).

<center>*Half Dwarfs.*</center>

Fillbasket and numerous varieties—Bateson (1).

Ringleader, Ceylon Native No. 2 (?), Satisfaction—Lock (54).

Express, Serpette, Plein le Panier (Fillbasket), numerous varie-
ties—Tschermak (81).

Autocrat, Bountiful—Keeble and Pellew (49).

Numerous varieties—White (unpublished data).

<center>*Dwarfs.*</center>

Numerous varieties—Bateson (1).

Eclipse—Hurst (42).

Ceylon Native No. 2 (?), Earliest Blue and others—Lock (54).

Couturier, numerous varieties—Tschermak.

Nott's Excelsior, Laxtonian and others—White (unpublished data).

<center>RESULTS FROM CROSSING.</center>

Most of the crosses involving height were not grown with enough
regard to environmental conditions, so that the data, although plenti-
ful, are valuable only for making broad generalizations. In crosses
between talls and dwarfs, the F_1 is generally even taller than the
tall parent.

Talls × talls gives only talls in F_1 and succeeding generations.

Talls × half dwarf give talls in F_1. In F_2 Tschermak (81) ob-
tained 48 talls; 18 half dwarfs or a ratio of 2.3 : 1. Bateson (1, 3)

apparently secured all three classes in some cases in F_2, *i. e.*, tall, dwarfs and half dwarfs. Lock (54) secured only talls and half dwarfs, but the half dwarfs were of two types in some cases—those with a relatively small number of long internodes and those with a relatively large number of short internodes. The talls were made up of a large number of long internodes.

Talls × dwarfs in F_1 give talls, often considerably taller than the tall parent. In F_2, talls and dwarfs appear in a ratio approximating 3 : 1. Lock (54), Hurst (42), Bateson and others have confirmed Mendel's original results. Mendel obtained in F_2 from a total of 1,064 plants, 787 talls and 277 dwarfs or a ratio of 2.84 : 1. Of 100 F_2 talls, 28 bred true in F_3, while 72 F_2 talls gave both tall and dwarf offspring, approximating a ratio of 2 : 1. The dwarfs bred true. Two more generations of this cross were grown by Mendel without securing exceptional results.

Half dwarfs × half dwarfs gives in F_1 in some cases only half dwarfs, or talls due to heterozygosis (1, 54) which give rise in F_2 and succeeding generations to half dwarfs. In other cases (49), involving a different set of varieties, the F_1 is extremely tall, while the F_2 generation consists of talls, two types of half dwarfs and dwarfs in a ratio approximating 9 : 3 : 3 : 1. Keeble and Pellew crossed two half dwarf varieties differing for the most part in only three characters—length and number of internodes and in diameter of stem. Thick stems, short internodes in large number (I.) × thin stems, long internodes in small number (II.) gave in F_1 plants with thick stems, long internodes in large number. In F_2, 5 F_1 plants gave rise to 192 progeny of 4 types as follows:

	Tall.	Half Dwarf (I.).	Half Dwarf (II.).	Dwarf.
Actual....................	114	33	32	13
Expected	108	36	36	12
Ratio....................	9	3	3	1

The dwarfs in this particular case all had thin stems and short internodes.

Half dwarfs × dwarfs in F_1 in some cases give intermediates (1, 3); in other cases half dwarf height is dominant. In a case of the latter type, Tschermak (81) obtained half dwarfs and dwarfs in F_2 and the dwarfs remained constant in F_3.

Dwarfs × dwarfs always gave dwarfs in F_1 and succeeding generations.

INTERPRETATION.

The inheritance of height in peas is an extremely important subject from a practical standpoint and well worth a most detailed and thorough study. In most cases, data now obtainable are extremely fragmentary and too general in character. However, so far as our present knowledge goes, two factors are involved and according to Keeble and Pellew—one (T) determines stem thickness, while the other (Le) gives rise to long internodes. The combination of TLe produces talls in F_1 and F_2, while the absence of these factors in F_2 gives dwarfs with thin stems. Many dwarf varieties have thick robust stems, though all known to me have comparatively short internodes and only few in number. Hence it seems to me that T stands not for thickness of stem but as a factor for large number of internodes. Interpreted in this manner, the formulas for various heights in pea varieties would be:

Tall, large number of long internodes, TTLeLe,
Half dwarf, large number of short internodes, TTlele,
Half dwarf, small number of long internodes, ttLeLe,
Dwarf, small number of short internodes, ttlele.

Both the interpretation of Keeble and Pellew as well as the one just given fail to account for the usual results from crossing talls and dwarfs. If talls are bifactorial in composition, in F_2, instead of talls and dwarfs being the only classes, half dwarfs should be extremely common, while dwarfs would appear not more than once in every 16 segregates. However, the classification of F_2 populations involving talls and dwarfs has been based in all probability in most cases on the length of the internodes, all segregates with long internodes, regardless of number, having been classed as talls, while those with short internodes were classed as dwarfs. In this way, the usual 3 : 1 ratio would be obtained, as only the factor Le is involved. The length of the internodes are shortened by the absence of the factor Fa and increased in number. This explains the talls with a large number of comparatively short internodes. As pointed out by Bateson (1), the groups designated talls, half dwarfs and

dwarfs are composed of many pure lines differing in a minor degree as to height, number of internodes, etc.

7. FASCIATION, UMBELLATE INFLORESCENCE.

Most varieties of peas have either robust or slender, angular or roundish stems, which are small at their base and three or four times the basal diameter at their top or flowering region. The flowers of such varieties are in ones, twos or threes on axillary peduncles along a large stretch of the stem. These are the *common* or " normal " characteristics of peas.

Fasciation in peas greatly alters the above characters by increasing the maximum width of the stem at the top from 1 cm. to as much as 4 cm. The stem in this region either presents the appearance of a flattened, pressed cylinder or of an irregular cylinder, with side splits and an opening in the top. Leaves as well as branches grow out from this inside tissue region. The leaf arrangement or phyllotaxy ceases to be regular in the fasciated region of such plants, and the flowers instead of being axillary are bunched together at the top of the stem in what may be called an irregular umbel or bouquet. Not uncommonly in these fasciated plants, growth is so uneven on opposite sides of the stem as to cause a curling up of the stem making it resemble one side of an Ionic capital or a ram's horn. Both Lobel and Gerarde mention and picture a fasciated variety of pea in their herbals, and according to all observers the character is strictly hereditary. In my own experience, seed of a fasciated variety obtained from Eckford of Wem, England, has always bred true to fasciation under every and all sorts of conditions. Fasciation does appear in other plants and in peas, however, which is not inherited, but is mainly due to environmental conditions. Further this type (8.5) is morphologically indistinguishable from the inherited type. Blodgett (8.5) cites a case in which 90 per cent. of the peas of fields grown for canning purposes were afflicted with this trouble, making the crops worthless except for green manure purposes, since fasciated peas bear but few pods and only when conditions are just exactly right. I have seen this same type of fasciation in greenhouse cultures a couple of times.

VARIETIES STUDIED.

Irish Mummy of H. Eckford, Wem, England. This is the common fasciated variety, which in the seed catalogues of different countries takes different names. In England fasciated varieties are called crown peas. I have experimented with several other fasciated varieties which were obtained from Russia and Sweden.

RESULTS FROM CROSSING.

Fasciated stems, umbellate inflorescence × non-fasciated stems, axillary inflorescence gives in F_1 absolutely "normal" stems with axillary inflorescences. In F_2, Mendel obtained from 858 plants, 651 with normal stems and axillary inflorescences and 207 with fasciated stem and umbellate inflorescences—a ratio of 3.14:1. Lock (56) and others have confirmed Mendel's results, although Lock notes there is considerable variation in the degree of fasciation in the segregates. Bateson and Punnett (3) secured various intermediate types in F_2.

Mendel carried his study of this cross through the F_4 generation. In F_3, of 100 "normal" F_2 plants, 33 bred true to normalness, while 67 gave both normal and fasciated plants in a 3:1 ratio. In F_4 no exceptional results were obtained.

INTERPRETATION.

Considering only genetic results, the hereditary difference between "normal" stemmed and fasciated stemmed peas is the presence and absence of a single factor Fa. When Fa is present, the stems are normal. In its absence, they are fasciated.

8. LEAF AXIL COLOR.

Generally associated with leaf axil color is color at the point of attachment of the pinnæ, colored margins in the young leaves and color at the base of the stem. The color is either red associated with pink flowers, or reddish purple associated with reddish purple flowers. Owing to changes in environment, particularly the amount of sunlight, the color varies in intensity even among the axils of the same plant. Although always associated with colored flowers and

colored seed coats, there are forms of *Pisum* with colored flowers and unpigmented axils. In the absence of pigment, the leaf axils and other structures noted above are greenish white or yellowish green, with which are associated white flowers and colorless seed coats.

VARIETIES STUDIED.

Colored Axils, Colored Flowers.

Purple Sugar Pea, Purple-podded Pea, Irish Mummy (*P. sat. umbellatum* or Egyptian Mummy, Crown pea, etc.), Purple-flowered Field Pea—Lock (54, 56).

English Gray Field Pea—Darbishire.

Graue Riesen (Purple Sugar), Svalöf *P. arv.*, Nos. VI., VII., VIII., IX., X.; Red-flowered Kneifelerbse and others—Tschermak (81, 86).

Non-colored Axils, Colored Flowers.

Svalöf *P. arv.*, No. IV.—Tschermak (86), Tedin.

P. humile ?, *P. quadratum* ?—Sutton (74).

Non-colored Axils, White Flowers.

A large number of white-flowered varieties have been used in studying inheritance of axil color. Among them are,

Laxton's Alpha, Veitch's Perfection, Sunrise, British Queen, Victoria Marrow, Très nain de Bretagne and others—Lock (54, 56).

Victoria Marrow, Emerald, Yellow-podded Sugar Pea, and others—Tschermak (86).

RESULTS FROM CROSSING.

Colored axils, colored flowers × non-colored axils, colored flowers in F_1 gave all colored axils, colored flowers. In F_2, Tschermak (86) obtained in such crosses,

Actual, 132 colored flowers and leaf axils: 49 colored flowers, non-colored leaf axils.

Ratio,   2.7 : 1
Expected,   135.75 : 45.25
Ratio,   3   : 1

Colored axils, colored flowers × the same always breeds true in F_1 and succeeding generations.

Colored axils, colored flowers × non-colored axils, white flowers gives in F_1 colored axils, colored flowers. In F_2 the following results have been obtained:

Investigator.	C. Ax., Col. Fl.	Non-C. Ax., White Fl.	Ratio.
Mendel............	705	224	3.15 : 1
Lock..............	184	65	2.83 : 1

In F_3, Mendel grew the progeny of 100 of the F_2 colored flower, colored axil segregates and found 36 bred true, while 64 again gave both the F_2 classes in similar proportions. In F_4 Mendel secured no exceptional results.

Lock's results (56) from selfing F_2 colored flower, colored axil segregates confirmed Mendel's results, part of them breeding true and a greater proportion giving both classes again.

Back-crosses of F_1 × colored flowered, colored axil parent gave all progeny with colored flowers and axils.

F_1 crossed with a white-flowered, non-colored axil variety gave 44 progeny with colored flowers and axils and 26 with white flowers.

F_2 white-flowered segregates × pure-colored flower, colored axil varieties gave all colored flower, colored axil offspring.

Non-colored axils, colored flowers × the same breeds true.

Non-colored axils, colored flowers × non-colored axils, white flowers in F_1 gives all colored flowers and colored axils. In F_2, Tschermak (86) obtained from a population of 545:

Class.	Col. Fl., Col. Ax.	Col. Fl., Non-Col. Ax.	White Fl., Non-Col. Ax.
Actually obtained............	336	83	126
Actual ratio.................	9.8	2.5	3.7
Theoretically expected........	306	102	136
Theoretical ratio.............	9	3	4

The proportion of segregates with colored flowers and colored axils to those with colored flowers and uncolored axils was 336 : 83 or 4 : 1, whereas the theoretically expected proportions were 314.25 : 104.75 or 3 : 1.

Extracted white-flowered segregates derived from the splitting up in later generations of the F_2 segregates with colored flowers and

non-colored axils, crossed with either colored flower, non-colored axil segregates or with the pure ancestral colored flower, non-colored axil variety always gave progeny with no color in their axils.

White flowered races crossed with each other never have given progeny with colored axils.

Interpretation.

All the data so far obtained indicate that color in the leaf axils, pinnæ, and stem base are explainable on a two factor basis, one of the factors (C) being absolutely coupled with the pink pigment flower factor (A). The other factor (D) is inherited independently of A or of any other factor so far as our present data go. Since A and C are absolutely coupled, it is simpler to consider them both as one factor (A). Regarded thus, colored axils result from the joint activity of A and D. In the absence of D, the plant will have no axil color, though the flowers and seed coats may be colored or non-colored (white). The factor D may be present in varieties with colored flowers or varieties with white flowers. Interpreted in this manner, all the above data are simply explained and all the various combinations mentioned may be obtained. The formulæ for the various varieties of peas would then be:

1. Colored flowers, colored axils $\begin{cases} \text{AAbbDD} \\ \text{AABBDD} \end{cases}$

2. Colored flowers, non-colored axils $\begin{cases} \text{AAbbdd} \\ \text{AABBdd} \end{cases}$

3. White flowers, non-colored axils $\begin{cases} \text{aaBBDD} \\ \text{aaBBdd} \end{cases}$

Tschermak (86) has given the formulas for 7 varieties with colored flowers and 5 varieties with white flowers. All the white-flowered varieties so far experimented with are aaBBDD, the aaBBdd class being represented only by Tschermak's true-breeding segregates from crosses of 2 × 3.

9. Flower Color.

Flower colors in all the cultivated varieties and species of peas are easily separated into three sharply defined classes, between which there are no intergrades. These color classes are white, salmon

pink, and reddish purple. The wild forms of *Pisum* most closely related to our common cultivated forms all have colored flowers of the reddish purple class. This last class is the only one in which the color varies according to the variety. The degree of variation is small and largely confined to a small group of wild or near wild Asiatic varieties of which *P. humile* Boiss. and *P. humile* ? of Sutton (74) are wild types. In this group of purple-flowered forms, the colors are dull and of about the same shade in both standards and other parts of the flower, the common purple-flowered forms being bi-colored (*i. e.,* lighter color shades in the standards). Benton is the most pronounced in light-colored standards of any of the bi-colored purple-flowered sorts. Environmental changes commonly met with in pea cultures have very little modifying effect on flower color, though wet, cloudy weather causes pink-flowered plants to produce white flowers.

VARIETIES STUDIED.

A large number of varieties have been studied, many of which are designated under the sections devoted to leaf axil and seed coat color. Reddish purple and white-flowered varieties are most commonly cultivated. The pink-flowered variety most easily procured is " Irish Mummy," known also as Mummy, Egyptian Mummy, *P. sat. umbellatum,* etc. Many field peas and " sugar pod " peas have colored flowers while the great majority of the garden peas are white-flowered.

RESULTS FROM CROSSING.

Lock (56) and especially Tschermak (84, 86) have given admirable summaries of the work on this set of characters, making it unnecessary to go into great detail here.

Purple flower × purple flower gives only purple-flowered offspring in F_1 and succeeding generations.

Purple flower × pink flower in F_1 gives all purple-flowered offspring, which in F_2 give both purple- and pink-flowered segregates in proportions approximating the 3 : 1 ratio. In F_3, the pinks and part of the purples breed true, the remainder again breaking up in the expected Mendelian proportions.

Purple flower $\times$ white flower in F_1 give all purple-flowered progeny. In F_2, generally only purple- and white-flowered segregates in an approximation to the 3 : 1 ratio are obtained. Mendel's results from a total of 929 F_2 were:

705 purple red : 224 whites or a ratio of 3.15 : 1.

In F_3 the whites tested and approximately one third of the 100 tested purple reds bred true, while about two thirds (64 F_2 ind.) gave purple reds and whites again.

In crosses of certain true breeding white segregates with purple-flowered races, purples are obtained in F_1, while in F_2, purples, pinks and whites occur in proportions approximating 9 : 3 : 4.

Pink-flowered varieties crossed with each other generally give nothing but pinks in F_1 and succeeding generations.

Pink flower $\times$ white flower in F_1 commonly gives all purple-red-flowered offspring, which in F_2 give purples, pinks and whites in a ratio of 9 : 3 : 4. Lock (56) and Tschermak (86) obtained the following results:

	Purple.	Pink.	White.	Total.
Lock	141	43	65	249
Tschermak..............	407	104	155	666
Total.................	548	147	220	915
Expected	514.35	171.45	228.6	

In F_3, the F_2 whites and part of the F_2 purples and pinks breed true, but the greater proportion of the latter two classes break up again, the purples giving either purples, pinks, whites; purples and whites, or purples and pinks, while the heterozygous pinks only give pinks and whites in a ratio of 3 : 1, the actual results obtained by Lock (56) being 113 pinks : 50 whites. Out of 16 F_2 pinks 6 bred true in F_3 while 10 were heterozygous for pink and white.

Back-crosses of the F_1 of this cross with pure white-flowered varieties gave 44 purple and 26 white-flowered plants, the theoretically expected being 35 of each. Back-crosses of this same purple F_1 with the pure pink strain gave 21 purple and 17 pinks, where an equal number of each was expected. Back-crosses of F_2 purples and whites with pure white and pure pink varieties gave results showing there were two genetic sorts of whites.

White flower × white flower always gives white-flowered progeny.

Tschermak has carried out and published (84) the results of a very complete series of back-crosses of F_1's, F_2's, F_3's, F_4's and F_5's with pure varieties and of the segregates of each type from several of these generations with each other. This work of Tschermak's, together with that of Mendel and Lock has put the genetics of flower color in *Pisum* on a very strong basis of fact.

All these and other studies on *Pisum* flower color have shown colored flowers to be always associated with colored seed coats, colored leaf axils, indent seed, etc., while white-flowered races are always characterized by their absence. Further, of the two colored flower types, purple flowers are always associated with reddish purple axil color and purple dots on the seeds, while pink-flowered varieties are associated with reddish leaf axils and reddish dots on the seed coat. Both purple- and pink-flowered forms are known or have been obtained through crossing which lack axil color or dotted seed coats, though all have the gray-brown seed coat for which the factor Gc stands.

Exceptional Cases.—In several cases both Tschermak and Fruwirth have secured purple flowers in F_1 from crossing two pink-flowered plants, where only pink was expected. Tschermak tentatively regards these pinks which give rise to purples as individuals which were really purples genetically, but for some reason the union of the factors A and B failed to produce purples when they were expected. Later B became active again. These exceptions are still under investigation.

INTERPRETATION.

According to Tschermak, flower color in peas is due to the presence and absence of two factors—a chromogen factor A and a color modifier or blueing factor B. When A only is present the plants have salmon-pink flowers, when both A and B are present the pink color is modified to a purplish red. When both A and B are absent the flowers are white. When A is absent and only B is present the flowers are also white, so that B cannot express itself in the absence of A. All white-flowered varieties so far tested have shown the

presence of B by giving purple flowers in F_1 in crosses with the pinks. Tschermak and Lock, however, have obtained true breeding white-flowered segregates lacking this factor.

When the necessary factors for axil color and dotted seed coats are present together with A, these respective regions are red pigmented, which if B is added, are modified to purple. In the light of the present genetic data, then, varieties of peas in respect to flower color have the following formulas:

Purple flowers ....AABB
Pink flowers ....AAbb
White flowers ....aaBB
White flowers (segregates only) aabb

10. TIME OF FLOWERING.

Varieties of peas vary from about 35 to 150 days or more in the time it takes them to reach the flowering period from the date of planting, when all are planted the same day and grown under similar conditions. As might be expected, different varieties of peas react somewhat differently to changes in environment as regards the time it takes them to reach the blooming period. Grown in 10 cm. pots in the greenhouse in the winter time this period is considerably lengthened in several varieties, while with other varieties there is practically no change—the same length of time being required as in the field cultures. Between the earliest and the latest blooming varieties, there is a continuous range of varieties with blooming periods at most not more than four days apart, so that in a random collection of a hundred varieties, one might record another variety in bloom almost every day. Between the individuals of a variety such as are many of the dwarfs, the individual variation in time of flowering is small, ranging over three to four days. Among the so-called "half dwarfs" and tall varieties, individual variation within the variety has a much wider range. Dwarfness, although generally associated with earliness, is also associated with medium late blooming varieties, but tall varieties are but very rarely early bloomers.

Lock (54), Tschermak (85) and Hoshino (40.5) have each

noted that white flower color is genetically associated with earliness while colored flowers are associated with late flowering. The association is not of an absolute nature in either case, as some of the latest flowering forms such as Späte Gold are white-flowered. None of the earliest varieties, however, have colored flowers, but this may be a coincidence, since varieties with colored flowers have not been selected for earliness and early flowering forms may have arisen which remained unnoticed.

Horticulturists and seedsmen divide varieties of peas on the basis of time of bloom into early, second early, medium, medium late and late. This classification is too general for scientific purposes, though of much practical value.

VARIETIES STUDIED.

Numerous varieties—Tschermak (85).

Ceylon Native No. 1, French Gray Sugar Pea—Lock (54).

Bountiful, Autocrat—Keeble and Pellew (49).

Victoria Marrow, various Finnish and Russian Field Peas—Relander (66).

"Early White-flowered Dwarf," "Late French Large-podded," "Mans"—Hoshino (40.5).

RESULTS FROM CROSSING.

Crosses of an earlier flowering variety with a later flowering variety generally give an intermediate in F_1 in this respect. Relander (66), however, finds that if the flowering periods are very close together the F_1 blooms at or very near the same time as the earlier flowering parent, but where the blooming periods are far apart, only intermediates are obtained in F_1. Keeble and Pellew (49) secured intermediate F_1's from crosses of two varieties with flowering periods about a month apart. In Tschermak's (85) crosses, the F_1's were either intermediate or near the late flowering parent. In one case the F_1's were all as late flowering as the late flowering parent. In Hoshino's crosses, the F_1 was nearest the late-flowered parent. In all studies of F_1 crosses in respect to flowering time, the numbers have been extremely small, Relander and Hoshino employing the largest.

In F_2, the usual result is a complete or almost complete intergrading series with occasional small breaks. The classification of such a series into early, intermediate and late is generally arbitrary, though often based on the blooming period of the two parents and the F_1 when these are grown under the same or similar conditions. With such a method of classification, Tschermak obtained from crosses involving seven different varieties, the following results:

Actual,　60　early : 190 intermediate : 88　late,
Expected, 63.3 early : 190 intermediate : 84.4 late,
Ratio,　　3　　　：9　　　　　　： 4.

Keeble and Pellew from crosses involving two varieties obtained 63 early : 128 intermediate : 1 late. Lock (54), classifying them in three 5-day frequency classes, obtained 63 early : 186 intermediates : 279 late.

Lock (54), Tschermak and Hoshino (40.5) have noted an F_2 association between colored flowers and lateness on the one hand and white flowers and earliness on the other. The modifying relation or coupling, whichever it may be, is only partial, as the following F_2 results show:

Class.	Early.		Intermediate.		Late.	
Flower color ....white		purple	white	purple	white	purple
Tschermak	25	22	48	94	4	64
Ratio	1 :	.88 :	1 :	1.96	1 :	1.16

White flowers : purple flowers 77 : 180 or 1 : 2.34.

Lock 29	34	79	107	104	175
Ratio .... 1 :	1.17	1 :	1.35	1 :	1.68

Purple flowers : white flowers 383 : 123 or 3.13 : 1.

The expected relation of the purple- to the white-flowered class, providing there was no coupling, is of course 3 : 1 in each of the classes—early, intermediate and late.

Tschermak (85) and Keeble and Pellew (49) have obtained some curious results regarding the relation of tallness and dwarfness to the time of flowering. In the one case (Fig. 3B) given by Tschermak the F_1 is tall and almost as late flowering as its late-flowering parent. In F_2 32 talls and 10 dwarfs result. Classifying

the talls by their blooming time, the result is 9 early : 15 interme-
diate : 8 late. The 10 dwarfs were 6 intermediate : 4 late, no earlies
being obtained where most expected.

Keeble and Pellew found lateness in blooming correlated with
short internodes and earliness with long internodes. Classified on
this basis, their results are:

Class.	Early.	Intermediate.	Late.
	53L : 10S	93L : 35S	0L : 1S
Normally expected ratio.....	3 : 1	3 : 1	3 : 1

Classified so as to show the relation of both the character of the
stem (thin or thick) and the length of internodes to time of bloom,
the results were:

63 Early	*128 Intermediate*	*1 Late*
22TL	92TL	—
2Tl	31Tl	—
31tL	1tL	—
8tl	4tl	1tl

Providing neither linkage (coupling) nor modifying effects were
present, *i. e.,* independent both in inheritance and development, the
theoretically expected ratio in each of these classes is 9 : 3 : 3 : 1.

In F_3, Tschermak found some of the F_2 earlies and all lates
remained constant or bred true. Some of the early class gave both
early and intermediate. The intermediates in some cases bred rela-
tively true, in other cases giving intermediates and lates and in still
other cases giving all three classes.

In several cases in F_2 and F_3, segregates flowering either earlier
than the early ancestor or later than the late flowering ancestral
variety, were obtained and these remain constant in later generations.

The F_4 generation results bore out the F_3 expectation.

Hoshino's studies involved 30,000 F_1, F_2, F_3 and F_4 generation
plants, and his results are similar to those obtained by Lock and
Tschermak, as regards flower color and time of flowering, but in a
cross between an early flowering dwarf variety and a late flowering
tall one, he found no evidence of coupling between the factors for

height and flowering time, as did Keeble and Pellew. An F_2 population from such a cross gave 23 ED:89 ET:76 LD:183 LT (Table I.).

INTERPRETATION.

Tschermak has provisionally interpreted his results as due to the presence and absence of two factors, with the possibility of there being a third, although he states this character is probably much more complicated.

The two factors are a " Zug " or pulling factor and a " Treib " or driving factor, there being possibly two of the latter. The " Zug " factor produces intermediates with a tendency to be late-flowering, while the " Treib " factor modifies the " Zug " factoral expression so as to give early flowering forms. By itself, it cannot alter the *status quo*. In the absence of both, constant late-flowering forms are produced.

The second " Treib " factor postulated is a positive present in all peas, giving constant lates in the absence of the other two factors or constant earlies in the presence of the other factors. The various varieties experimented with, on the two factor conception, would be represented by formulæ as follows:

> Constant early ....AABB,
> Constant intermediate...........AAbb,
> Constant late ....aaBB or aabb.

Combinations of AABB × aabb would give in F_1 an intermediate AaBb. In F_2 the expected ratio of early, intermediates and lates would be 3:9:4. Further explanation is long and complicated. In view of the numberless varieties with differences in the length of time it takes them to reach the blooming period, it appears to the writer that some cases should be of simpler composition than others—the early, intermediate and late classes being interpretable as combinations of a single pair of factors, which in F_2 would give a 1:2:1 ratio.

Hoshino (40.5) also interprets his genetic data on time of flowering by means of two factors, one of which, Lf (A), determines the " proper " time of flowering in the late parent, while Ef (B) modifies the expression of Lf toward earlier flowering, and is hypo-

static to Lf. The absence of Lf is epistatic to the absence of Ef, and determines the time of flowering of the early parent, while the absence of Ef causes the early variety to bloom a few days later. Gametic contamination of some sort is believed to be involved, but the factors are distinctly stated not to be "inconstant" in the sense in which Castle (10) uses the term. Lf ("A") is partially coupled with factor A for flower color, the proportion of non-cross-over to cross-over gametes approximating 7:1.

11. Number Flowers per Single Peduncle.

Flowers in *Pisum* are borne either singly, in twos or in threes on a single axillary peduncle, unless the factor for normal stem is absent. *P. elatius* is an excellent example of the "flowers per peduncle 2–3" type, while most of the commonly cultivated varieties are two-flowered or 1–2-flowered. Such early forms as Velocity, First of All, and Black Abyssinian are almost totally single flowered.

According to Hurst (44), the tendency to bear pods (and consequently flowers) in pairs is inherited. Vilmorin (90) states 1-flowered and 1–2-flowered peduncles to be dominant to 2–3-flowered peduncles, these two characters being determined by the presence and absence of a single factor. In the table, this is designated Fn. Strictly one-flowered types and their relation to the 1–2-flowered type apparently have not been studied.

12. Foliage and Stem Color.

The foliage and stem color of peas is either green or yellowish green, each color generally being associated with unripe pods of the same color, although a few purple and yellow podded varieties of peas are known with green leaves. Green or purple podded yellow-leaved varieties are unknown. Gold von Blöcksberg and Goldkönig are typical yellow-leaved varieties.

The writer obtained from crossing yellow foliage, etc., × green foliage, etc., green foliage, green podded F_1 progeny, which in F_2 gave 681 with green foliage, green pods and 222 with yellow foliage, yellow pods, the expectation being 677:226. Of 45 green foliage,

green podded F_2 segregates tested in F_3, 14 bred true, while 34 gave both yellow and green foliage and podded F_3 progeny, the total ratio being 427 GF : 146 YF. 15 F_2 yellow-foliage segregates gave all yellow-foliage F_3 progeny. F_4 gave no exceptional results.

INTERPRETATION.

Varieties with green foliage and green pods differ from those with yellow foliage in the form investigated by the presence of the factor O. Hence all varieties of peas investigated with green foliage are OO, while those with yellow foliage are oo.

13. TENDRILLED AND NON-TENDRILLED LEAVES.

With one exception, all cultivated varieties of peas have leaves in which part of the pinnæ have been replaced by tendrils. This one exception—the Acacia variety—has wrinkled seeds and no tendrils, the place of the tendrils being taken by extra pinnæ. The variety breeds true as regards both the characters mentioned. Its origin is unknown, though the variety was first studied by Vilmorin (89, 90).

RESULTS FROM CROSSING.

Tendrilled, round seed × Acaciā, wrinkled seed gave in F_1 all tendrilled, round-seeded progeny. In some crosses, the F_1 tendrils are slightly strapped-shaped, especially in the youngest tendrilled leaves. Otherwise dominance of tendril is complete.

The F_1 plants bore F_2 round and wrinkled seeds in the usual 3 : 1 proportions and the F_2 proportion of tendril and Acacia plants was as expected, approximately 3 : 1. In such a cross, providing these two pairs of characters were independently inherited, four classes in a ratio of 9 : 3 : 3 : 1 would be expected. When the seed and leaf characters were thus considered the four expected classes were found, but the proportions were awry, the two middle classes being all but absent. In other words, the F_2 round seeds gave almost exclusively tendrilled plants, while the F_2 wrinkled seeds gave practically all Acacia or non-tendrilled plans, showing that round and tendrils, wrinkled and Acacia were almost completely linked or coupled together in their inheritance.

In the F_2 generation, or from heterozygotes of the same composition as F_1, the following results have been obtained:

Investigator.	Round Seeds Gave		Wrinkled Seeds Gave	
	Tendril.	Acacia.	Tendril.	Acacia.
Vilmorin................	113	2	5	70
Vilmorin (case 2)..........	170	1	4	99
Bateson.................	210	4	1	64
Pellew (64)...............	1466	20	15	564

The first three series of results are less accurate than that of Pellew because the classification of rounds and wrinkleds was not made by examining the starch, hence errors occurred—wrinkleds being sown for round and *vice versa*. By the starch examination method, there could be no such mistakes, as wrinkleds *always* have " compound " or much split roundish starch grains.

Tendrilled wrinkled × constant round-seeded Acacia segregates (64) gave in F_1 the usual results, but in F_2, the round seeds gave 502 tendrilled, 270 Acacia, while the wrinkled seeds gave 264 tendrilled, 0 Acacia.

Pellew tested out other pairs of characters with tendrils and Acacias to see if there was any coupling, but none was found. Among these pairs tested were tallness and dwarfness, yellow and green cotyledons, purple and white flowers, glaucous and emerald foliage and fasciated and normal stems.

INTERPRETATION.

The factor (R) for roundness of seed, etc., and its absence (r) for wrinkled seed, etc., have already been considered. Tendrilled and non-tendrilled plants (Acacia) are due to the respective presence and absence of the factor Tl. The peculiar ratios obtained as regards both sets of factors show that partial linkage or coupling exists between R and Tl on the one hand and r and tl on the other. The interpretation of the manner in which this partial coupling is brought about is too extended to consider here. Suffice to say that Bateson (3.5) and his students explain it by somatic segregation and the increased rapidity of growth of the germ cell area which is to give rise to the large classes, as compared to that which gives rise to

the small classes. This is called the reduplication hypothesis. Morgan and his students (61, 62, 73) explain the same facts in a wholly different manner on the basis of the linear arrangement and "linkage" of groups of factors together in the same chromosome, and the occasional crossing-over of factors to the opposite or homologous chromosome during the maturation divisions. To the writer, the latter appears to be the more simple interpretation and better supported by the facts.

14. Bloom.

With comparatively few exceptions, all varieties of peas have a waxy surface covering on their leaves, stems, pods and other plant parts. The varieties from which this is absent are known as Emeralds and very easily become diseased. Emerald varieties studied by Vilmorin (89) are Emereva, Johnson's British Empire and Pois à brochettes.

Results from Crossing.

Glaucous (waxy) $\times$ glaucous gives glaucous.

Glaucous $\times$ emerald in F_1 is always glaucous (89, 86, 92). In F_2, the following results have been obtained:

Investigator.	Glaucous.	Emerald.	Total.
Vilmorin	138	39	177
Tschermak	35	18	53
Actual	173	57	230
Ratio	3	1	
Theoretically expected	172	57	

In F_3, of 15 F_2 glaucous, 5 gave all glaucous, while 10 gave 133 glaucous: 32 emeralds. 15 F_2 emeralds tested in F_3 gave all or 199 emeralds.

Emerald $\times$ emerald (89, 92) gave glaucous in F_1 which in F_2 gave glaucous to emeralds in the ratio of 9 : 7. Vilmorin crossed Emereva (emerald) with two other emeralds noted above with the same results. The following results were obtained from 2 F_1 plants in F_2:

Plant A,   27 : 20 emerald,
Plant B,   23 : 21 emerald.
Actual,   50 : 41
Calculated, 51.1 : 39.8

In F_3 6 F_2 glaucous plants gave in one case all glaucous, in 5 cases both glaucous and emerald. Of 3 F_2 emeralds tested in F_3, only emerald progeny resulted.

INTERPRETATION.

The above data show that two factors are involved in the inheritance of bloom; in the absence of either or both, the plant is emerald. No emeralds have been obtained as yet in which both factors for bloom are absent. Regarded thus, in respect to bloom and its absence, varieties of peas with bloom are BlBlWW, while emeralds may be either blblww, BlBlww or blblWW. Emeralds of the first type should be obtained as segregates.

15. PRODUCTIVENESS.

Productiveness is to be regarded as a composite character or one made up of a very large number of other characters. Length of vine, number of internodes, number of pods per single peduncle, number of pods per plant, length of pods, number of pea ovules per pod, number of peas matured per pod are a few of the hereditary characters, the combined results of which are called productiveness. In addition to these there are a host of environmental conditions which either raise or lower the hereditary productivity of a variety. For a scientific study of the heredity of productiveness, it is necessary to eliminate as nearly as possible variation caused by environment, and this is most easily accomplished by growing the varieties to be studied and their hybrids under as near as practicable, one set of conditions. A study of this character under these conditions, so far as I am aware, has not yet been published.

Varieties of peas, as well known, differ remarkably in the average number of pods they bear, and these variations are governed, as usually studied, quite as much by environment as by heredity. Such early varieties as Morning Star, Excelsior, Velocity and others do

well under ordinary conditions if they average four pods per vine, while some of the late varieties with large vines may average 30 to 50 pods. Variation in the number of pods per single vine is large even among the individuals of a pure varietal strain, but in some cases this may be regarded as almost entirely environmental. Further the extremes as to few or large number of pods never transcend certain limits, and supposedly these limits represent the character of the environment, whether most unfavorable or most favorable. Olin (63) records a plant grown in the Colorado mountains under exceptional conditions which was 3 meters high and bore 650 pods averaging 5 peas per pod. On the other hand, some of the wild forms average 4 pods per plant.

Hurst (44) grew 112 varieties under about the same conditions. From data on these, the heaviest yielders appeared to be those varieties with the largest number of pairs of pods, but he states this to be more apparent than real. Some varieties generally bear pods singly, while other varieties have them in pairs or in threes. Twenty plants of Velocity gave Hurst 202 singles and no pairs, while a score or more of plants of other varieties gave all the way from 4 doubles: 471 singles to 142 doubles: 593 singles.

Shaw (70) from a large series of biometrical studies on several pea varieties came to the conclusion that the number of pods per single plant was not a heritable character, but that it was correlated with vine length, which is heritable. Shaw's experiments and treatment of his material, however, were not of such a character as to throw much light on this subject. Shaw and others point out the probability that each node is potentially capable of producing pods. In most modern studies of heredity, however, one considers only the physical characteristics of a plant or a variety as they actually are under a given set of environmental conditions and not the potentialities or possible variations of this plant or variety under a thousand and one environments in which it might be grown.

The productivity of any variety of pea, as is well known, is increased by harvesting the green marketable pods, instead of allowing the first crop to mature.

Relander (66) has begun a careful study of the problem of productivity in peas by growing the parents and crosses in pots of

similar size and soil contents under the same environmental conditions and taking data on the total dry plant, seed and straw weight per pot, weight per 1,000 seeds, the average number of pod-carrying internodes and pods per plant and the average number of seeds and seed "Anlagen" or ovules per pod. In crosses between varieties or pure lines differing in these respects, the F_1 progeny gave various results, depending on the varieties crossed and the character considered. In all crosses, the individuals of one pure line culture of the variety Victoria were used as one of the parents, the other parents being from pure lines of Russian and Finnish field pea varieties. The F_1 results as given by Relander are in figures with which figures from the two parent varieties are given for comparison. Table A roughly represents the character of the F_1 progeny in terms of the parent characters. Intermediate means only approximate intermediate condition, Relander's figures showing that the productivity in most of the cases marked intermediate was nearer that of the more productive parent.

TABLE A.

DIFFERENT F_1 VARIETAL CROSSES.

Character.	I.	II.	III.	IV.	V.	VI.
Total weight of dry plant per pot......................	H.E.P.	Int.	Int.	H.P.	H.P.	H.P.
Total seed weight per pot....	H.E.P.	Int.	Int.	H.P.	H.E.P.	H.E.P.
Total straw weight per pot...	Int.	Int.	Int.	H.P.	L.P.	Int.
Weight per 1,000 seeds (only fully mature, well-developed seed used)................	Int.	Int.	Int.	Int.	Int.	Int.
Ave. no. of pod carrying internodes per plant	H.P.	L.P.	Int.	L.P.	Int.	Int.
Ave. no. pods per plant	H.P.	H.P.	H.P.	Int.	Int.	Int.
Ave. no. seeds per pod.......	Int.	H.P.	H.P.	H.P.	H.E.P.	H.E.P.
Av. no. of ovules or seed "Anlagen" per pod............	All intermediate but nearer the high producing parent. No data on No. VI.					

H.E.P. = Higher than either parent.
  H.P. = Dominance of more productive parent.
  L.P. = Dominance of less productive parent.
  Int. = Intermediate.

Relander interprets the differences in her results as due to differences in factorial composition of the different varieties she used. She does not believe that the increased productivity obtained in

certain of her crosses is due to heterozygosis in the sense of East and Hayes (27).

16. Pod Color.

As regards color of unripe pods, varieties of peas may be classified into three groups—green-podded, yellow-podded and purple-podded.

Green-podded varieties are the most common and are typical of all the wild species. Green pods are never associated with yellow foliage.

Yellow-podded varieties often have bright yellow pods associated with yellow flower-bearing axes, green stems and foliage. All yellow-foliaged varieties, such as Goldkönig and Gold von Blöcksberg, have yellow or yellowish green pods. All yellow-podded varieties known to me have yellow cotyledons, although segregates have been obtained with yellow pods, yellow foliage and green cotyledons.

Purple-podded varieties such as Nero and Purple-podded Field Pea have colored flowers and gray seed coats. Tschermak (86) cites Vilmorin as saying that weak purple pigmentation has been found in pods on white-flowered plants. Lock (56), Tschermak (86) and Fruwirth (34) have found considerable variation among different pods of the same plant, some pods being wholly purple, while others are purple splashed with green in various degrees. Plants with all purple pods are also found. Fruwirth attempted to secure by selection a stable pure green-podded race from the green and purple-splashed podded plants. Ten generations gave entirely negative results. Strains having only purple pods were secured in these same experiments by planting seeds of wholly purple pods. Fruwirth regards the appearance of these true breeding purple-podded strains as bud mutations.

Results from Crossing.

Green pod × green pod always gives green pod (pure varieties).

Green pod × yellow pod gives in F$_1$ all green-podded progeny. In F$_2$ Mendel secured approximately 3 green-podded plants : 1 yellow-podded. Tschermak's results involving crosses of yellow pod

with 8 very distinct varieties with green pods confirmed Mendel's results. In some of these crosses, Tschermak obtained colored-flowered, yellow-podded segregates which remained constant. Yellow-pod segregates always bred true, while the green-pod F_2 segregates in F_3 in some cases were constant, and in others gave both green- and yellow-podded plants.

Green pod $\times$ purple pod in F_1 always gives all purple-podded progeny (56, 86, 34, 90). In F_2, Lock obtained five different types of segregates—segregates with all purple pods, with all green pods, and segregates having green pods with various degrees of purple coloring. Some plants were very faintly pigmented. Tschermak obtained small F_2 numbers—10 purple in different degrees: 5 green. In F_3, the F_2 purple-pigmented plants gave 34 purple : 27 green. Fruwirth, on the other hand, obtained all green-pod progeny in F_1 of two crosses of green pod $\times$ purple or purple-splashed pod varieties, and in F_2 of one of them, 39 green-podded and 10 purple or purple-splashed segregates were obtained. According to Fruwirth, purple pod color is inherited independently of purple-specked seed coat pattern.

Yellow pod $\times$ purple pod gives in F_1 (86) purple pod, which in F_2 gives purples or purple-splashed : yellow in an approximation to a 9:7 ratio. Yellow-podded segregates always breed true.

No data have been published on crosses of F_2 yellow and F_2 green-podded segregates from combinations involving purple-podded varieties.

<div align="center">INTERPRETATION.</div>

So far as our present data go, all green-pod varieties of peas may be regarded as differing from yellow-pod varieties by the presence of a factor Gp. The factorial relation of purple-podded varieties to green- and yellow-pod varieties cannot be cleared up until more data are obtained. Tschermak regards purple-pod varieties for the present as bifactorial, differing from green- and yellow-pod races by the presence of two factors (P_1 and P_2). Through the presence of both of these factors purple-pigmented pods would result. In the absence of either or both the plant has green or yellow pods. Possibly there is more than a bifactorial difference between purple- and yellow-podded varieties, but Tschermak's num-

bers are too small to throw much light on this possibility.   Purple-podded varieties need a much more thorough study before putting them on a factorial basis.   Green- and yellow-podded varieties may be provisionally represented as the presence and absence of Gp.

17. Pod Apices.

Varieties of peas have either blunt (obtuse) or acute pods. Most curved varieties such as Black-eyed Marrowfat and Scimitar have acute pods, while blunt pods are characteristic of Nott's Excelsior, Gold von Blöcksberg, French Gray Sugar, Ringleader and others.   These characters are generally most sharply defined in well-filled pods.   In many varieties doubtful pods occur on the same vine with those easily classified.

Results from Crossing.

Blunt (*stumpy*) × acute in F_1 always gives all blunt-podded offspring (81, 1, 54, 56).   In F_2, blunt-podded to acute-podded plants occur in approximately 3 : 1 proportions.

Interpretation.

The difference between blunt- and acute-podded varieties may be represented by the factor Bt, its presence denoting bluntness, its absence acute pods.

18. Parchmented or Non-Parchmented, Smooth or Constricted, Non-Edible or Edible Pods.

The great majority of pea varieties have pods the inner lining of which is tough, papery and membranous in both the mature and immature state.   The ripe or mature pods of these parchmented varieties are very tough and generally do not crumple up in drying. In the wild species this parchmented character is exceptionally well developed while in a few cultivated varieties such as the thin-podded Goldkönig, the parchment is comparatively inconspicuous, so that the dry pods are slightly crumpled.   None of these varieties are regarded as having edible pods.

Differing conspicuously from these parchmented varieties are

the so-called sugar peas. The pods of this group of varieties are absolutely non-parchmented, and more tender, sweet and edible than string beans. When unripe, the pods have a granular translucency and are crumpled and constricted, so that the peas as they mature appear to be pushing out that part of the pod with which they are in contact. When dry, these pods shrink and become much more constricted, and very brittle. As a green vegetable they are very popular in continental Europe and in China. So far as known no wild forms have this character, though cultivated varieties of it are described as far back as our botanical records go.

VARIETIES STUDIED.

Parchmented.—See Tschermak (81, 86), Darbishire, Bateson (1, 3), Lock (54) and others (89, 99).

Non-parchmented.—Wachs Schwert, French Gray Sugar, Petit Pois, Dwarf French Gray Sugar, Giant Sugar (pods up to 11.25 cm. long).

RESULTS FROM CROSSING.

Parchmented × parchmented always gives parchmented in F_1 and succeeding generations.

Parchmented × non-parchmented in most cases gives complete dominance of parchment in F_1 (60, 86, 89, 90). In other cases, different varieties being used, the F_1 has been more or less intermediate, *i. e.,* parchmented but not as heavily as in the parchmented parent (1, 56).

In F_2, the proportion of plants with either fully parchmented or with more or less parchmented pods to those with complete absence of parchment in their pods approximate 3:1. The following results have been obtained:

Investigator.	Parchmented.	Non-parchmented.	Ratio.
Mendel	882	299	2.95 : 1
Tschermak	45	15	3 : 1
Lock........................	59	25	2.3 : 1
Totals, 1,325..............	986	339	2.9 : 1

Tschermak, Lock and Bateson have made many crosses involving these characters but the actual numbers are given in only a few cases. Bateson (1) and Lock (54, 56) both obtained intermediates in some crosses.

In F_3, from seed of 100 parchmented F_2 plants, Mendel found 29 that bred true and 71 that had both parchmented and non-parchmented offspring. The non-parchmented F_2's always bred true. In F_4, no exceptional results were obtained.

Mendel, Lock and Tschermak have always found parchmented pods to be inflated and non-parchmented to be constricted.

Non-parchmented × non-parchmented in some cases give only non-parchmented in F_1. In other cases (Vilmorin 89) in a large series of crosses between diverse varieties of non-parchmented peas, the F_1 progeny have been frequently parchmented. In F_2 these parchmented F_1's have produced approximately 9 parchmented : 7 non-parchmented progeny.

INTERPRETATION.

Parchmented varieties of peas may be regarded as differing from those having non-parchmented pods by the presence of either one or two factors (P and V). No varieties or tested out segregates have been recorded representing the absence of both P and V, but from Vilmorin's results one should expect to find them. All parchmented varieties may be regarded as PPVV, while non-parchmented varieties so far investigated are either PPvv or ppVV. PPvv × ppVV would give parchmented F_1's and 9 parchmented : 7 non-parchmented in F_2, while either PPvv or ppVV × PPVV would give parchmented F_1's and a 3 : 1 ratio in F_2.

19. ADHERENCE BETWEEN MATURE PEAS IN THE POD.

As well known, all varieties of peas except one have pods in which the seeds are entirely free from each other. This one exceptional variety known as "Chenille" has pods with free immature seeds, which when mature adhere more or less closely to each other as though stuck together with glue, and this particular char-

acter under favorable environmental conditions is completely hered-
itary. The variety was sent to Vilmorin from Switzerland in 1906
by M. Frommel and had emerald leaves. It has been suggested that
the absence of wax (glaucousness) has been partly responsible for
its origin, as the young growing peas in contact with each other, free
from wax, tend to grow together as do grafts. But in other emerald
varieties the peas do not adhere, so the attempted explanation is
not very satisfactory.

RESULTS FROM CROSSING.

Free seeds, glaucous foliage, pink flowers × chenille seeds,
emerald foliage, white flowers gave in F_1, glaucous foliage, purple-
red flowers, and free seeds. In F_2 a total of 175 progeny gave 144
with free seeds and 31 with adherent seeds or a ratio of approxi-
mately 4:1. Considering the combinations of this pair of charac-
ters with those of flower color and foliage character in F_2, the
results were:

Plants glaucous (138) { flowers colored   105 } seeds free
                        { flowers white   33 }

Plants emerald   (39) { flowers colored 29 { chenille 28
                                              { free   1
                        { flowers white   8 { chenille   3
                                              { free   5

These results show all is in accordance with ordinary Mendelian
theoretical expectation both as to classes and numerical representa-
tion of classes, until the chenille and free seed pair of characters
is considered. Here one notes (1) that glaucous plants have only
free seeds whereas on a one-factor basis about 35 plants are ex-
pected to have chenille seeds; (2) that the chenille and free seed
characters are distributed among the emerald plants in approximately
3:1 proportions, but just the reverse of what ordinarily would be
expected, the dominant character in F_1 in this cross being free
seeds.

In F_3 the F_2 plants of various kinds tested out gave as follows:

Character of F₂ Parent.	No. of F₂ Plants Tested.	Character of F₃ Progeny by Classes.							
		GCF.	GCA.	GWF.	GWA.	ECF.	ECA.	EWF.	EWA.
GCF......	4	no chenilles							
GCF......	5	45	1	12	1	1	19	1	2
GWF	1	no chenilles							
GWF	5	—	—	70	4	—	—	4	5
ECA......	9	—	—	—	—	4	81	2	7
ECF......	1	—	—	—	—	9	6	2	2
EWA	3	—	—	—	—	—	—	40	30
EWF	1	—	—	—	—	—	—	10	6

G = glaucous, E = emerald, C = colored flowers, W = white flowers, F = free seeds, A = adhering or chenille seeds.

Free seeds, emerald foliage × chenille seeds, emerald foliage (both parents white flowered) gave in F_1, free seeds and glaucous foliage. In F_2, 50 glaucous non-chenille, 39 emerald non-chenille and 2 emerald chenille were obtained or 89 with free seeds to 2 with chenille seeds. In F_3, the tested F_2 segregates gave:

Character of F₂ Parent.	No. F₂'s Tested.	Character of F₃ Progeny.			
		GWF.	GWA.	EWF.	EWA.
GWF	1	all	—	—	—
GWF	3	45	—	15	—
GWF	2	20	—	15	3
EWF	1	—	—	all	—
EWA	2	—	—	33	17

INTERPRETATION.

The only explanation so far offered for these perplexing results is that by the Hagedoorns (38.5), in which the factor S (A) represents free seeds and its absence chenille seeds. The presence of either or both of the factors for glaucous foliage, Bl and W, is unfavorable for the expression of "chenille." Only plants of the formula sblw (abc) normally give chenilles, in other words plants with emerald foliage from which S (A) is absent. The factors responsible for broad non-parchmented pods and colored flowers in association with the sblw combination is favorable to the production of chenilles, while the blueing factor B which transforms pink flower color into purple red flower color is unfavorable because it also darkens the color of the seed coats. Environmental conditions are also modifying agents. The presence of the factors for broad

non-parchmented pods makes a decided difference in the number of chenille plants that are obtained in crosses. Seeds of purple red flower segregates are said to rarely cohere, even though the plants are sblw (abc).

It seems to the writer, however, that these results are more plausibly and simply interpreted as partial coupling or linkage of the factor S with either Bl or W, it being impossible to tell which until further data are obtained. The amount of crossing over is shown by the following grouping of the F_2 progeny and that of certain heterozygote families in F_3:

Linked, 90–97%.	Total.	Crossovers, 3.3–10.5%.	Total.
GF, 138 + 57 + 70	265	GA, 0 + 2 + 4	6
EA, 31 + 21 + 5	57	EF, 6 + 2 + 4	12

The percentage of plants with emerald foliage is much lower than that expected on a 3 : 1 ratio, and as chenille seeds and emerald foliage are coupled, this also brings down the per cent. of chenilles below the theoretical expectancy. Emeralds in the writer's experience as grown from seed kindly sent by P. Vilmorin, succumb much more easily to disease than the general run of glaucous varieties and perhaps this accounts for the low per cent. of emeralds obtained in Vilmorin's hybrid generations. The relation of flower color to free and chenille seeds is not clear on the present scant data, though the evidence does not favor the idea of partial coupling between one of the color factors and chenille, so far as the writer can discover. The approximation between the obtained frequencies (152 RpF : 48 RpA : 51 WF : 6 WA) and those theoretically expected (144 : 48 : 48 : 16) indicate either independent inheritance or at most very loose coupling.

20. POD DIAMETER.

Both pod diameter and pod length in peas present the same complex mixture of environmental and genetic variations as is found in such characters as time of bloom, productivity and height. Several of the wild varieties have the smallest and most narrow pods (0.8–0.9 cm.) while the sugar peas have the longest and widest

(2.0–2.6 cm.) pods. Between these two extremes are numerous varieties with pods representing all gradations in size, each variety having pods with a definite range of variation characteristic to it, when the varieties compared are grown under similar environmental conditions. The following list of varieties (by number) with their green pod diameter range will give a clearer idea of these differences:

P43	0.8–0.9 cm.	P24	1.5–1.5 cm.
P35	1.1–1.1 cm.	P92	1.5–1.6 cm.
P12	1.2–1.3 cm.	P14	1.5–1.6 cm.
P87	1.2–1.3 cm.	P116	1.5–1.7 cm.
P123	1.2 cm.	P31	1.5–1.7 cm.
P83	1.3–1.5 cm.	P81	1.5–1.6 cm.
P72	1.4–1.6 cm.	P32	1.6–1.8 cm.
P76	1.4–1.5 cm.	P60	2.0–2.5 cm.
		P82	2.0–2.6 cm.

RESULTS FROM CROSSING.

Tschermak (81) and Lock (54, 56) crossed narrow-podded peas with wide-podded varieties and obtained in F_1 either intermediates or dominance of the large pod type.

In F_2, segregation was observed but the plants were extremely difficult to classify as the pod width per plant distribution gave a continuous series. For example, Lock crossed 13 mm. $\times$ 20 mm. and obtained 18 F_1 plants with pods of the following character:

Mm. frequency classes	12	13	14	15	16	17	18	19	20
No. of plants				3	6	6	2	1	

In F_2, 32 plants were grown, giving the following frequency distribution:

Mm. frequency classes	12	13	14	15	16	17	18	19	20	21
No. of plants	1	2	5	4	8	5	6	1		

In F_3, the narrow pod segregates did not breed true. Large seeds were to some extent correlated with wide pods.

In another cross (13 mm. $\times$ wide-pod Telephone), 14 F_1 plants had pods on the average as wide as those of Telephone. In F_2, 78 plants gave the following distribution.

Mm. frequency classes	12	13	14	15	16	17	18	19	20	21
No. of plants		5	14	9	17	22	9	2		

In the F_2 of a reciprocal of this same cross, 42 wide and intermediate and 13 narrow were obtained. A correlation between narrow pods, small seed and leaves and wide pods, large seeds and large leaves is noted.

In still another cross of the 13 mm. variety × French Sugar (over 20 mm.), the F_1 pods were intermediate. Of 84 F_2 plants, 19 were classified as narrow-podded and 65 as wide-podded.

In F_3, seeds of the various F_2 types gave

9 F_2 narrow pod produced only narrow (13–16 mm.),

4 F_2 narrow pod produced very narrow and narrow pods,

9 F_2 wide pod produced only wide (17 mm. and over),

22 F_2 wide pod gave both narrow and wide pods.

In this cross, as in the others, wide pods in the main were associated with large seeds and narrow with small seeds.

INTERPRETATION.

Lock (54) interprets his data as showing segregation in F_2, but until a much greater mass of data is obtainable, it is useless to speculate on the factorial nature of this character. In some cases one should expect a simple one factor difference, while in other cases the results are probably very complex.

21. MATURITY OF GREEN PODS FOR MARKET.

This character is complex and closely associated with the time of blooming, etc. Hurst found a variation of 52 days among the 112 varieties he grew under similar environmental conditions. Tedin (77) crossed varieties of peas breeding true to the same ripening period and secured forms with decidedly longer and shorter time of maturity periods.

STERILITY.

Sterility in peas is almost unknown even in crosses between such so-called species as *P. arvense, P. Jomardi, P. elatius, P. sativum.* The only recorded cases of sterility in this group are between a form

of *P. humile* Boiss. (Sutton, 74) and various varieties of *P. arvense*
and *P. sativum.* Sutton made 40 crosses, using in each case *P. humile* as one parent and 10 varieties of white-flowered (*P. sat.*)
and 7 of colored (*P. arv.*) as the other parents. The results were
various, but apparently each combination produced seed. When
planted some failed to germinate or died immediately after germina-
tion, others reached the flowering stage but no seed were produced
and still others produced seed, which failed to germinate. In a few
cases, the F_2 seed germinated, and the plants flowered but no seed
resulted. In four cases, the F_1 plants were completely fertile, two
of the hybrids having white-flowered *P. sativum* ancestry and 2
having colored-flowered *P. arvense* ancestry.

In crosses involving this same form (the seed of which Mr. Arthur
Sutton kindly sent me) and forms of *P. elatius, P. sativum* and *P. arvense,* the writer obtained plants completely fertile in F_1. In the
crosses, however, great difficulty was experienced in making them
" stick," and the majority of cross pollinations resulted in failure.
Many of the F_1 generation seed failed to germinate, though only
plump seed were planted.

MUTATION.

As compared with such organisms as the pomace or fruit fly,
Drosophila mutations are very rare in peas. All horticulturists and
breeders remark on the extreme constancy of pea varieties, some
of which have been in existence for at least a quarter of a century
without showing any striking modifications, and one variety, the
British Queen, is said by Sherwood to be practically a century old.
Several of the varieties mentioned by Darwin (22), such as Victoria
Marrow, Pois géant sans parchemin, Scimitar, Auvergne, Champion
of England, are still in existence to-day and very little changed, so
far as one may decide by the descriptions written in his day. Tedin
(77) who has made detailed studies of a large number of varieties
at Svalöf and who is on a special lookout for mutations has found
them rare and none of them of much practical value.

Fruwirth (34) in conducting selection experiments on a variety
of pea with pods and seeds varying in all degrees in the amount of
purple pigment it possesses, discovered a very curious type of bud

mutation. The pods on a single plant generally varied from pure purple to purple streaked with green. Plants with all purple pods also occurred. The seeds were either pure yellowish green, yellowish green with purple flecks, purple with small yellowish green flecks, or wholly purple. Seeds of all these colors occur together on the same plant or even in the same pod or each type occurred pure on single plants. Pedigree cultures for ten generations showed that bud mutations or sports arose whereby pure strains were established with yellowish green seeds. Other bud sports or mutations gave rise to true breeding purple-podded strains. That these were not the result of selection as is ordinarily understood by that term is shown by their abrupt origin and their breeding true at once.

Another mutation of the same type is the wild vetch-like " rogue " which many varieties of cultivated peas throw in varying percentages. Bateson and Pellew (5) have investigated the genetics of this " rogue " mutation with the following results: The varieties investigated were Ne Plus Ultra, Early Giant and Duke of Albany. Thoroughly typical plants of these varieties occasionally throw rogues and intermediate forms. The rogues, when fertile (rarely sterile), have exclusively "rogue" offspring. The intermediates from typical plants give a mixed progeny of a few typical plants and many " rogues." Some varieties and some strains of the same variety throw more " rogues " than others. Selected Gradus strains throw about one per cent., while some varieties such as Fillbasket appear never to throw rogues. Rogues crossed with rogues always give rogues.

These two cases of mutation appear to be similar to what Emerson (27.5) calls, in cases investigated by him in corn, "recurring somatic variations," or what East (26.2, pp. 40–43) refers to as recurring mutations, meaning of course that it is impossible to free a variety from the recurrence of the mutation (in East's case, semi-starchy seeds in varieties and segregate lines of sweet corn).

If mutations are so rare in peas as our present knowledge seems to indicate, how have all the numerous genetic differences among them come about? In the absence of records, so far as can be judged from what has been observed in other organisms, it is most plausible to believe that most of the so-called factors originated as

mutations and were subsequently shuffled among a large number of forms, largely through artificial crossing. From the lack of intermediates and from their Mendelian behavior, it is almost inconceivable that such characters as non-parchmented pods, lack of tendrils, pink flowers and emerald foliage could have originated in any other manner.

SELECTION.

In the American Cyclopedia of Horticulture, under peas, L. H. Bailey states that varieties of peas left to themselves soon lose their distinctive characteristics, because of their great variability. This statement is contrary to all the information I have found in the writings of English horticulturists and others on peas (22, 42, 51, 57.5, 96, 72). In fact, most of our new varieties of peas are obtained through crossing, there being so little variability in varieties by which one may bring about improvement through selection.

In the work at the Svalöf Experiment Station, improved varieties are secured through selection, but in reality this is simply isolation of pure lines which have either arisen unnoted as mutations, or as unselected segregates from crosses far back. Tedin's (24) character basis by which he isolates new forms is the average weight of seeds, their number per pod and the total number of pods per plant, etc. Upon isolation, these new forms immediately form constant varieties.

Fruwirth (34) is the only one who has made a modern scientific study of selection in peas. The Blauhülsige variety, as already stated, has either wholly purple pods or purple pods streaked with green. Both color types occur on the same plant and some plants have only purple pods. The seeds of this variety are pure purple, purple flecked with greenish yellow, yellow green flecked with purple or wholly greenish yellow. All types occur on the same plant or each on separate plants, but the progeny of each type give rise to all the other types. After 10 years of pure line selection and 2 years of mass selection for a pure purple-seeded race, no results have been secured. Selection toward a pure constant green-seeded race also resulted in failure. Selection for the same length of time toward a pure constant green-podded race gave only negative results.

"ROGUES."

The term "rogue" is applied by seedsmen to any variation or off-type plants in a field of pure-bred plants of a variety. For example, tall peas in a plot sown to dwarf peas, colored-flowered individuals in a white-flowered variety, yellow seeds in a green-seeded variety, late bloomers in an early-flowering variety are all designated as rogues and carefully eliminated. In many cases, these rogues are due to careless handling of the seed; in others, to the presence of heterozygotes which subsequently produce recessives— the heterozygotes having arisen through rare insect crossing or through never having been selected out when the variety was first placed on the market, e. g., Nonpareil and others with yellow and green cotyledons. Again, these "rogues" may come about through "recurring mutation" phenomena or through regular mutation. In Tschermak's studies on flower color and maple seed coat, certain factors appeared in exceptional cases to be present but inactive. Thus among pink-flowered peas, plants with purple red flowers might occasionally appear. Still another way in which "rogues" could easily occur has its basis in a change in environment and in the fact that all factors or factor combinations do not react alike to such changes, so that while under one environment a variety might breed true, under another, variations would appear, due to unsuspected factorial differences.

Most of these rogues can be eliminated permanently by removing the cause, but those that result from recurring mutations can, so far as we now know, only be reduced to a minimum and kept there only by constant watchfulness.

COUPLING (LINKAGE) AND CROSSING-OVER.

Varieties of peas so far investigated have seven pairs of chromosomes (Cannon, 11). If the genetic factors of animals and plants are located in the chromosomes as believed by Morgan (62) and others (61, 62.5, 26.5, 73), all the factors of a single variety of peas should be inherited as though linked or coupled together in seven groups, each group representing the factor composition of one of the seven pairs of chromosomes. This grouping in peas can be determined with the least trouble by crossing a variety having seven

or more different factors with a variety lacking these factors, mak-
ing the cross a sufficient number of times to insure a large F_2 popu-
lation (4^7 or 16,384 individuals at least) or by making all the pos-
sible combinations of the seven-factor pairs through separate cross-
ings.   In F_2, in the former case, if each factor is inherited inde-
pendently of all the others and large enough numbers of progeny
are grown, there should be 128 F_2 combinations which remain con-
stant in F_3 and later generations and 2,187 combinations all together
(60), each of which would be represented in a definite proportion of
the progeny.   Each of the seven factors should be present in ap-
proximately three fourths and absent in one fourth of the total
offspring.   If 8 factor differences were involved, the various numer-
ical terms would be proportionally increased.   But in the event that
a cross involving 8 factors did give the theoretical expectation for
the independent Mendelian segregation of eight pairs of factors,
the chromosome theory, as at present held, would either be dis-
proven or modified, for there would be only seven pairs of chromo-
somes involved in carrying the eight pairs of factors through the
mazes of the maturation divisions, where segregation is believed
generally to take place.

More accurate data on this subject are obtainable by back-
crossing the F_1 hybrids with the recessive classes, but back-crossing
in peas on a large scale is impracticable, as so few seeds are obtained
from each cross.   The large size of pea chromosomes, as compared
to those of *Drosophila,* may be assumed to indicate, on present
theories, a looser linkage of the factors of each group, as compared
with the close linkage of the *Drosophila* groups.   This loose linkage,
if it exists, increases the difficulties of classifying the factors in
groups and in determining their relation to each other within the
group.

Inheritance studies on *Pisum* so far have disclosed only four
linked groups of factors (ACEGcL₁Lf, RTl, GO, SBl or SW), and
several other doubtful groups in which some of the factors are not
as yet clearly delineated.   In the first group, the evidence is com-
plete enough to show the coupling is absolute except for the factor
Lf and hence for simplicity's sake, the first five factors may be
regarded as one.   G and O also appear to be partially coupled,

although the data are scant. R and Tl as shown by Vilmorin, Bateson and Pellew are only partially coupled, there being a small per cent. of the combinations rTl and Rtl in F_2. These are interpreted by Morgan and his students as cross-overs or combinations due to the simultaneous breaking of the chromosomes with respectively rtl and RTl at a point between the two kinds of factors and the subsequent union of the parts so as to bring r and Tl, R and tl together. This breaking occurred in about 1.5 per cent. of the total cases as regards the factors R and Tl. S and Bl or W are also in all probability partially coupled, similar to the case just described. The work of Morgan and his students on *Drosophila* has shown that by assuming that the linked factors of a group are arranged in an end-to-end straight-line series, definite places in the chromosome may be assigned to each factor, and their relative distances from each other may be given in terms of a standard unit equal to 1 per cent. of crossing-over. When a large number of the factors of a single chromosome have been studied the relative frequency of the cross-overs of the various factors may be approximately calculated and predicted.

When the relations in inheritance of the various factors to each other in such a group as *Pisum* are worked out, a definite basis for predicting correlation between different characters will have been found. On this basis, it will be possible to calculate with comparative ease the somatic characteristics of F_2 hybrid populations involving large numbers of factors, because so many of these characters will be associated together by linkage and may be considered as the expression of a single factor. Supposing the inheritance of a hundred factors in *Pisum* is involved in a cross about which it is desirable to have forehand knowledge. If each is independent of all the others in its inheritance, it is obvious that accurate predictions in regard to the combinations would be made with great difficulty, but if these are linked together in large groups, predictions can be made with fair accuracy and considerable ease.

Crossing-over makes predictions regarding F_2 hybrid populations somewhat more difficult than if the factor linkage was absolute, but at the same time they bring about new combinations in predictable proportions which, in a system where the coupling was absolute, would not be possible.

Further, on the chromosome-linkage-factor-crossing-over hypothesis, the amount of variation in a group of similar organisms (a species), eliminating that caused by environmental changes, would be in proportion (1) to the number of factor differences between the various forms or varieties of the group; (2) to the number of pairs of chromosomes; (3) possibly to the relative sizes of the chromosomes (small chromosomes making crossing-over much more difficult) and (4) to the amount of cross fertilization which took place (either natural or artificial).

As Morgan points out, the interpretations of the genetic data on *Drosophila* crosses advanced by him and his students hold whether the chromosomes are or are not the bearers of the factors.

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